Changing climate and the winter foraging ecology of Antarctic fur seal populations

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Declaration of Originality

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Abstract

Knowledge of the habitat use and foraging ecology of animals in space and time is fundamental to understanding the structure and function of their ecosystems, inter-relationships with earth and climate systems, and to inform management and conservation. The examination of relationships across ecological levels (individuals, populations, species) can reveal the effects of the intrinsic characteristics of individuals and extrinsic environmental factors, and contributes to a broader understanding of an animal's biology.

This thesis examines the foraging behaviours, habitat use and drivers of these for female Antarctic fur seals (*Arctocephalus gazella*) from three Southern Ocean colonies during the poorly studied austral winter, from the individual to the species level. The at-sea winter distribution of Antarctic fur seals from Marion Island, Bird Island and Cape Shirreff was quantified over six years (2008-13) using archival global location sensing (GLS) loggers, while time-depth recorders were used to record diving behaviour at Marion Island (2012 and 2013). Specifically, this thesis aims to (1) ascertain the degree of foraging site fidelity of seals, (2) use diving behaviour to identify foraging strategies and associated costs and benefits, (3) identify important winter foraging habitats of populations and their associated environmental characteristics and (4) quantify recent decadal changes to winter habitat and temporal variability in habitat use to facilitate assessment of the degree of overlap with Southern Ocean management areas and fisheries.

(1) Data from Marion and Bird Island animals was used to assess individual fidelity to oceanic foraging sites. Site fidelity was examined at two scales: within and between years. Within-year site fidelity was typically weak, indicating that successive

foraging trips over the winter target different regions in response to seasonal environmental changes. Conversely, between-year fidelity to foraging regions was strong for the majority of animals (>50% of the annual home range re-used), who returned to individually unique foraging grounds over multiple years. The major oceanographic parameter typifying areas of re-use was a high long-term (multi-decadal) variance in sea surface temperature, which is likely associated with elevated productivity and increased energy intake over the individual's lifetime. These findings show that foraging strategies not only vary between individuals, but also can persist over the long-term.

(2) Diving behaviour and fine-scale habitat use were examined during the post-breeding migrations of Antarctic fur seals by combining vertical and horizontal movement data. The relationship between movement responses across horizontal and vertical dimensions was assessed. A broken-stick approach, novel for otariid seals, quantified within-dive foraging effort and identified two distinct foraging strategies that presently co-exist in the Marion Island population: (i) remain north of the Polar Front close to the colony, or (ii) transit south of the Polar Front. The trade-offs associated with the two strategies are established and include habitat availability, accessibility to vertically migrating prey and travel costs. This work highlights the co-existence of divergent foraging strategies within a population and how determination of associated trade-offs can facilitate predictions of how strategies might be impacted by future changes to population size or environmental conditions.

(3) Habitat models (species distribution models) were developed for the three colonies based on GLS tracking data from 184 seals over six years to assess spatial distribution patterns and reveal the environmental factors influencing foraging areas at broad scales. The core habitats for each colony were identified, with several areas

of inter-colony overlap revealed. Population-level differences in winter foraging habitats and influential environmental parameters were observed, suggesting that populations are differentially influenced by their environment.

(4) The potential response of Antarctic fur seals to environmental change was examined by building on the habitat models. Past changes to influential environmental parameters were quantified and the baseline spatial distribution of foraging habitats for each colony was hindcasted. Despite notable regional changes to sea surface temperature, wind speed and sea ice concentration, foraging habitat has remained relatively consistent at Marion and Bird Islands, but a reduction in sea ice has improved habitat availability for the Cape Shirreff population. Spatio-temporally explicit models were developed to detail the temporal variations in foraging habitat that occur over the winter in response to environmental conditions, prey availability and energetic demands. Several important foraging habitats overlapped in both space and time with fishing effort, revealing a potential for competition and interaction with Southern Ocean fisheries for prey resources. Large amounts of foraging habitat was observed outside of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Convention Area, suggesting the impacts of fisheries and climate change can occur remote from the area of active monitoring and management.

By considering the inter-relationships between the habitat use and foraging behaviours of individuals, populations and the species, this study has produced new insights into the ecology of a major Southern Ocean predator during the poorly studied non-breeding winter, which are relevant not only to the ecology and management of Antarctic fur seals, but have broader applications for understanding the foraging decisions and demographics of marine predators and management implications for Southern Ocean ecosystems.

Statement of Publication & Co-authorship

Chapters 2, 3 and 4 are produced from manuscripts either published or in press in peer-reviewed journals. Chapter 5 is in preparation for submission to a peer-reviewed journal.

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

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The candidate was responsible for study design, data analysis (including the processing of the majority of geo-location data and state-space models which form part of a larger, ongoing tracking program), some fieldwork, interpretation of the results and manuscript preparation for the following manuscripts.

Paper 1 Arthur B, Hindell M, Bester M, Trathan P, Jonsen I, Staniland I, Oosthuizen WC, Wege M, Lea M-A (2015). Return Customers: Foraging Site Fidelity and the Effect of Environmental Variability in Wide-Ranging Antarctic Fur Seals. *PLoS ONE* 10:e0120888

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<u>Co-author contributions:</u> Mary-Anne Lea helped design the study, assisted with interpretation of results and contributed to manuscript production. Mark Hindell helped design the study, assisted with data analysis and interpretation and contributed to manuscript production. Marthan Bester undertook fieldwork. Phil Trathan helped design the study. Iain Staniland undertook fieldwork. Chris Oosthuizen undertook fieldwork. Mia Wege undertook fieldwork. Ian Jonsen assisted with data analysis.

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Chapter 5 of this thesis

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We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or accepted) peer-reviewed manuscripts contributing to this thesis:

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Chapter 1

General Introduction

Predators that occupy high trophic levels are an important component of most of Earth's ecosystems. Higher order, or top, predators are central to the structure and function of ecosystems through the consumption of large quantities of prey (Furness & Birkhead 1984; Boyd 2002), influences on the distribution and abundance of lower trophic level species (Schoener & Spiller 1996; Crooks & Soulé 1999), top down control through trophic cascades (Paine 1980; Estes *et al.* 2011) and the cycling and redistribution of nutrients (Schmitz *et al.* 2010). Top predators are crucial for ecosystem stability and there are numerous examples where the removal of predators has had far-reaching impacts throughout ecosystems (Estes *et al.* 1998; Dulvy *et al.* 2004; Myers *et al.* 2007; Baum & Worm 2009). Many species of large predators have been commercially exploited in the past and continue to recover since the cessation or reduction of harvesting (Lotze *et al.* 2011). The reintroduction of these populations into food webs will potentially have a range of impacts on the energy flows and trophic interactions of ecosystems (e.g. Ripple & Beschta 2003). Furthermore, as the effects of changes occurring at lower trophic levels are propagated and amplified up the food web they are reflected in the response of top predators, making them ideal indicator species of ecosystem health (Zacharias & Roff 2001; Hindell *et al.* 2003).

Foraging ecology and habitat use of marine predators

Many of the ecological concepts used in the study of marine predators were developed during research on terrestrial animals. For example, Optimal Foraging

Theory (MacArthur & Pianka 1966) seeks to understand the foraging strategies of animals under given conditions, while the closely aligned Marginal Value Theorem (Charnov 1976) extends this to consider how animals should forage in patchy environments. More broadly, niche theory (Hutchinson 1957) helps to define how an individual's or species' requirements and tolerances define the conditions and resources needed for survival. Population level concepts, including density dependent factors such as intraspecific competition, dispersal, philopatry and population size, and ecosystem level concepts such as trophic linkages and resilience, are all equally applicable to marine environments as they are to terrestrial systems.

In marine environments, information on the foraging ecology and habitat use of predators is fundamental to a broader understanding of the composition and function of their ecosystems. This information is also needed to inform and appraise management and conservation approaches such as fisheries management and by-catch mitigation (Burger & Shaffer 2008), the design of marine protected areas (Hooker & Gerber 2004), the identification of biological hotspots (Block *et al.* 2011) and ecosystem-based management (Hays *et al.* 2016). The development of accurate ecosystem models with which the effects of environmental changes can be better understood, also rely on quantifiable knowledge of the foraging ecology and habitat use of marine predators and the factors that influence and ultimately determine these.

Use of the ocean by foraging predators is not random. Rather their distributions and foraging decisions are driven by the availability of prey resources. In marine environments, prey is patchily dispersed in space and time (Russell *et al.* 1992), often in an unpredictable manner (Weimerskirch 2007). The distribution and abundance of marine prey is intrinsically coupled with physical and biological oceanographic properties, permitting us to link the biological responses of higher order predators with the fundamental biophysical properties of their environment (Bost *et al.* 2009). As direct measurements of prey availability (e.g. ship-based acoustic estimates) are rare in pelagic environments and typically do not have comprehensive spatial and temporal coverage, environmental proxies which characterise ocean processes related to prey abundance are often relied upon to better understand the distribution and foraging ecology of marine predators at regional scales.

One approach to link the distribution patterns of predators with the biophysical aspects of their environment is with habitat models. Once the environmental drivers of species distributions are identified, models may then be used to make predictions of habitat use in un-sampled areas (Elith & Leathwick 2009). For wide-ranging predators, where it is often difficult to sample the movements of many individuals or where high levels of intra-individual variability in habitat use exist, precluding population or species-level inferences from being made (Hays *et al.* 2016), this approach can be a valuable tool to make informed predictions of habitat use in remote pelagic environments. Habitat models for marine predators can also be extended to quantify the effects of environmental perturbations on the habitat use of species (Robinson *et al.* 2012). Historical distributions, which act as necessary baselines for understanding future changes (Lotze & Worm 2009) in the world's oceans, can also be estimated using this approach.

The foraging decisions of all animals should operate to minimise energy expenditure while maximising energy intake. In patchy habitats such as pelagic waters, foraging animals have to balance their rate of prey consumption with the energetic costs associated with travel and search times (Charnov 1976). In addition, individual animals are unable to perceive the entirety of their environment (Pyke

1984; Pachur *et al.* 2012). Instead, their knowledge of productive foraging regions is acquired over time. The patterns of movement observed in many marine predators are thought of as being optimal for locating patchily dispersed prey (Sims *et al.* 2008). For central place foragers (Orians & Pearson 1979), which repeatedly travel from a home point to distant foraging locations, it can be advantageous to return to an area that has previously been used successfully. Such fidelity to foraging sites is common where resource quality is predictable (e.g. flying foxes and flowering trees, Markus & Hall 2004). But where prey availability is unpredictable, fidelity to foraging sites may also present a longer-term energetic benefit (Perry & Pianka 1997). Examining the re-use of habitat by marine predators can aid in our understanding of their foraging ecology and spatial distribution patterns, in particular whether foraging strategies are consistent over time and whether long-lived individuals have the capacity to respond to future changes in their environment.

As the ocean is a three-dimensional environment, quantification of how animals use the water column is necessary for a comprehensive understanding of the habitat use and foraging ecology of a given species. Dive data can be informative in this context, as the diving behaviour of marine predators can vary markedly both between and within individuals in response to a range of factors such as region and habitat type (Nordstrom *et al.* 2013), age and experience (Fowler *et al.* 2006), reproductive status and associated energetic constraints (Scheffer *et al.* 2012), target prey (Miller & Trivelpiece 2008), the diel cycle (Shepard *et al.* 2006) and sex (Beck *et al.* 2003). On a finer scale, indices can be developed using diving information to infer foraging effort or success that is otherwise challenging to observe directly (Womble *et al.* 2013). Integrating this with location information can allow quantification of different foraging strategies and how marine predators use their three-dimensional environment.

The Southern Ocean

MARINE ECOSYSTEMS

The Southern Ocean is the oceanic region south of the Subtropical Convergence, incorporating Antarctic and sub-Antarctic waters. It is a complex oceanic system which is largely structured by the eastward flowing Antarctic Circumpolar Current, the flow of which is centred on frontal regions (Orsi *et al.* 1995) (Fig 1.1). The areas between fronts (inter-frontal zones) represent distinct water masses (Sokolov & Rintoul 2009a; Sokolov & Rintoul 2009b), which are commonly characterized by elevated productivity and biomass (Lutjeharms *et al.* 1985; Pakhomov *et al.* 1994) and are regularly targeted by foraging predators such as seals, penguins and albatross (Bost *et al.* 2009). The location of Southern Ocean fronts is not static, varying in relation to strong westerly winds and topography (Sokolov & Rintoul 2009a).

The Southern Ocean is further characterized by the presence of sea ice (Fig. 1.1), which can cover up to 20 million square kilometres of ocean during the winter (NASA 2014). Sea ice can have both positive and negative influences on the productivity and biomass of marine ecosystems in the region. For example, although phytoplankton abundance is typically poor in the Southern Ocean (Arrigo *et al.* 2008) significant plankton blooms occur in the seasonal sea ice zone (Moore & Abbott 2000) through several mechanisms including meltwater-induced stability and decreased turbulence within the mixed layer (Smith & Nelson 1986). The sea ice zone also supports sea ice algae which are important contributors to primary productivity (Lizotte 2001). In turn, the biomass of Antarctic krill (*Euphausia superba*) (Atkinson *et al.* 2004), a keystone species in the Southern Ocean ecosystem is directly linked to the primary productivity of the sea ice zone. Yet sea ice can attenuate solar radiation, reducing photosynthetic rates and impacting primary productivity (Arrigo & van Dijken 2011), as well as presenting a physical barrier to foraging animals (Ainley *et al.* 2003).

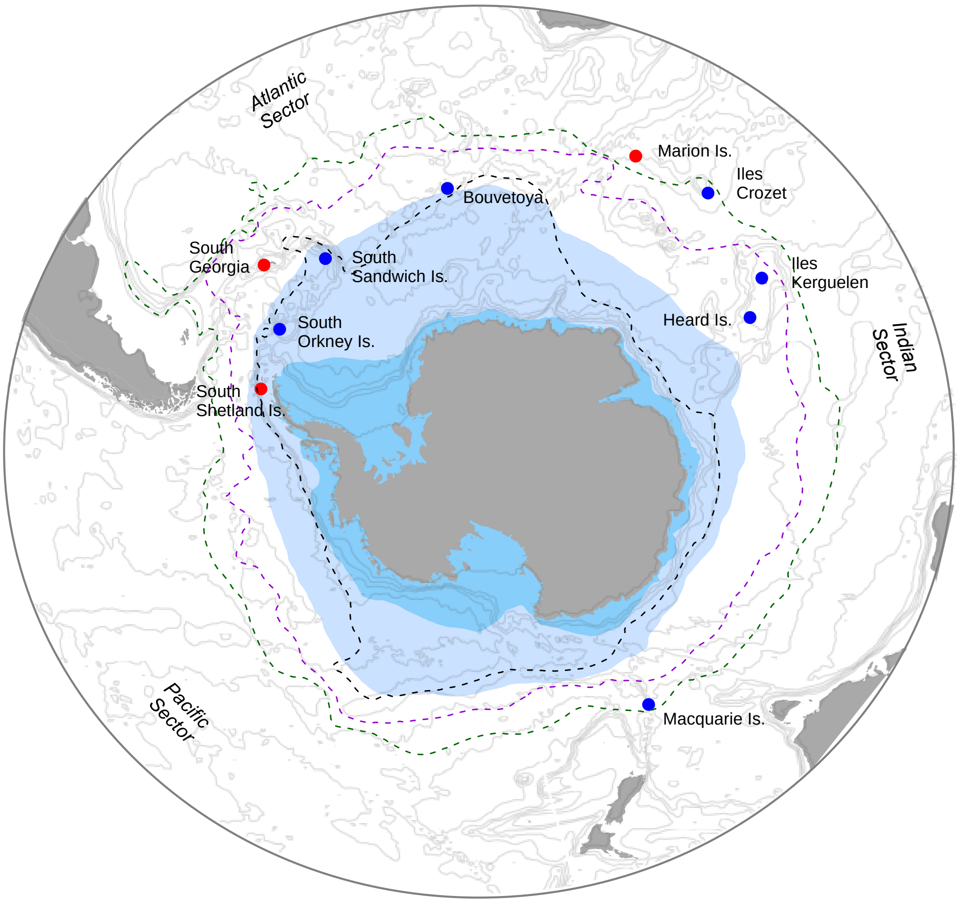

Figure 1.1. The location of Antarctic fur seal breeding colonies in the Southern Ocean. The study populations are shown by red circles, while remaining populations are in blue. The dashed lines represent the location of the sub-Antarctic Front (green), Polar Front (purple) and Antarctic Cirumpolar Current (black). The mean maximum winter and minimum summer sea ice extent (1979-2009) are shown in blue shading.

The major regions of productivity in the Southern Ocean include frontal zones, bathymetric features (shelf slopes, islands etc.), the sea ice edge and polynyas (Koubbi *et al.* 2014). The diversity of species is highly patchy (Griffiths 2010) yet overall, the area supports an exceptional biomass of higher-trophic level predators such as whales, seals and seabirds (Knox 2006). Predators inhabiting the Southern Ocean face a range of challenges to exist and reproduce in this extreme and highly dynamic environment. In addition to the obvious problems associated with extreme temperatures and photoperiodicity (Cockell *et al.* 1999), predators have to cope with highly variable levels of productivity (Moore & Abbott 2002) which affect food availability, as well as intense competition for prey resources (Ainley *et al.* 2006; Trathan *et al.* 2012) and sometimes breeding space (Hofmeyr *et al.* 2005) during the short summer reproductive season. In response, many predators have evolved a suite of adaptations to this environment ranging from physiological (e.g. thermoregulation in Emperor penguins Aptenodytes forsteri, Croxall 1997), metabolic (e.g. fur and fat stores in pinnipeds, Feldhamer *et al.* 2007), life history (e.g. large capital breeders vs smaller income breeders, Boyd 2000) and behavioural (e.g. seasonal migrations, Cockell *et al.* 1999).

SOUTHERN OCEAN CLIMATE CHANGE

The Southern Ocean is a rapidly changing environment. Some of the clearest and fastest large-scale physical changes anywhere on Earth are occurring here, including rapid rises in atmospheric and oceanic temperatures (Vaughan *et al.* 2003; Gille 2008), loss of ice sheet mass (Pritchard *et al.* 2012), changes to sea ice cover (Stammerjohn *et al.* 2008) and a south-ward shift in the position of frontal regions (Sokolov & Rintoul 2009b) and circumpolar westerly winds (Thompson & Solomon

2002). Despite well-documented changes to the physical structure of the Southern Ocean, it is less clear how the biological component of Antarctic marine ecosystems will be affected. There is, however, increasing evidence of anthropogenic changes in the distribution and abundance of prey through large-scale climate changes (Atkinson *et al.* 2004) and several studies have already documented changes in marine predator populations associated with the predicted effects of climate change (e.g. Barbraud *et al.* 2000; Weimerskirch *et al.* 2003; McMahon & Burton 2005). Nonetheless, the impacts of environmental changes in the Southern Ocean on top predators remain poorly understood overall.

SEASONAL VARIABILITY IN THE SOUTHERN OCEAN

Winter in the Southern Ocean is distinct both physically and biologically from the summer. The expansion of sea ice from the summer minimum to the winter maximum and back again is one of the biggest natural changes on Earth. This coupled with increased frequency of storms (Reeder & Smith 1998) and declines in primary productivity associated with decreased temperature and solar radiation (Clarke 1988; Mitchell *et al.* 1991), make the Southern Ocean in winter a challenging environment. The majority of Southern Ocean predators have weaned or fledged their offspring and departed their breeding colonies. During this time they are released from the constraints of provisioning their young and free to travel more broadly (e.g. Lowther *et al.* 2014). The movements, habitat use and foraging ecologies of Southern Ocean predators during winter, therefore, afford insights into habitat and prey preferences during an unconstrained period when foraging animals have more potential choice available to them. Considering these factors, the at-sea behaviour of predators in the Southern Ocean is expected to vary across the annual cycle. In particular, winter foraging behaviours are likely to differ markedly from the more constrained summer foraging patterns that are well documented for many species (e.g. Raymond *et al.* 2014 and data within). Yet until recently, the winter foraging ecology of many Southern Ocean predators has remained poorly studied. The use of animal-borne electronic tags to acquire information on location and behaviour (Ropert-Coudert & Wilson 2005) has proved vital in revealing the movements of marine animals in distant areas of the Southern Ocean. However, the majority of studies are biased towards the shorter summer period. Recent advancements in bio-logging technology such as improved battery life and memory capacity, increased miniaturisation of tags, reduced cost and the evolution of statistical methodologies (Evans *et al.* 2013) has permitted the tracking of a wider size variety of species for longer periods of time, including the Southern Ocean winter.

Antarctic fur seals

ABUNDANCE AND DISTRIBUTION

Antarctic fur seals (*Arctocephalus gazella*) are a numerous and key Southern Ocean predator. Historically the species was hunted for its fur and was driven close to extinction across its range by the 19th century (Bonner & Laws 1964). Since sealing operations ceased in the early 20th century, the species has recovered at different rates across its former geographic range. At South Georgia, which is thought to hold approximately 95% of the global population (Croxall *et al.* 1992), the annual rate of increase was as high as 16.8% between the 1950's and 1970's (Payne 1977). The total population is now estimated to be between 4.5-6.2 million (SCAR-EGS 2004). Other populations in the Southern Ocean experienced similar increases, although the rate of growth has now slowed or stabilised in some populations, others continue to increase (see SCAR-EGS 2004). Antarctic fur seals have recovered to breed at 10 principal sites across the Southern Ocean: South Georgia, South Sandwich Islands, South Orkney Islands, South Shetland Islands and Bouvetoya in the Southern Atlantic Ocean; Marion Island, Iles Crozet, Iles Kerguelen and Heard Island in the Southern Indian Ocean; and Macquarie Island in the Southern Pacific Ocean (Fig 1.1).

BREEDING BIOLOGY AND FORAGING ECOLOGY

Antarctic fur seals are one of the better-studied Southern Ocean predators. However, the vast majority of information concerns the summer breeding months. The breeding season commences in November when males arrive at colonies to establish territories. Females typically arrive in December and give birth to a single pup several days later (Doidge *et al.* 1986). Antarctic fur seals are considered 'income breeders' (Boyd 2000) as they rely on energy obtained on foraging trips during their extended lactation (Boyd *et al.* 1991) rather than energy stored in fat reserves as for 'capital breeders' (e.g. Grey seal, *Halichoerus grypus*). As the energetic demands of provisioning a growing pup increase, the duration of foraging trips by females lengthens across the season in response (Doidge *et al.* 1986). Pups are typically weaned by early autumn (March-April).

During the summer, Antarctic fur seals have a diverse diet, largely consuming krill, fish and squid in proportions that vary regionally. In the Atlantic sector the summer diet is dominated by Antarctic krill (Reid & Arnould 1996) with fish prey also frequently recorded (Davis *et al.* 2006), whereas the diet of populations in the Indian and Pacific sectors are dominated by higher-trophic level fish and squid (Goldsworthy *et al.* 1997; Klages & Bester 1998; Lea *et al.* 2002a).

The foraging behaviour and habitat use of Antarctic fur seals is well studied at this time of year, with the major foraging habitats of breeding animals well documented for many colonies (Goebel *et al.* 2000; Robinson *et al.* 2002; Bailleul *et al.* 2005; Lea *et al.* 2008; Biuw *et al.* 2009; Staniland *et al.* 2010). In addition, summer diving behaviour (Boyd & Croxall 1992; Arnould *et al.* 1996; Goebel *et al.* 2000) and the relationships between at-sea movements and local environmental conditions are also well understood; with factors including bathymetry, primary productivity and ocean temperature known to affect distribution and foraging activity (Guinet *et al.* 2001; Lea *et al.* 2006).

THE NON-BREEDING SEASON

The ecology of Antarctic fur seals during the non-breeding winter is poorly understood. Scat analysis has shown the winter diet of Antarctic fur seals consists mainly of krill and fish (Green *et al.* 1991; Reid 1995). More comprehensive analyses using stable isotopes have revealed the winter diet of females varies spatially and temporally, with differences in the trophic position of prey between habitats, colonies and months (Walters 2014). At South Georgia, Boyd *et al.* (2002) tracked 10 females during lactation and post-breeding, observing noticeable increases in foraging range upon the removal of breeding constraints. Staniland *et al.* (2012) further revealed the winter habitat use of 16 female Antarctic fur seals from South Georgia. These studies showed that female Antarctic fur seals can undertake wide-ranging foraging migrations during winter, in addition to documenting the importance of local South Georgia waters and the Patagonian Shelf to foraging animals. A more recent study has, for the first time, quantified the winter habitat use of Antarctic fur seals from other breeding colonies, revealing a diversity of foraging habitats and strategies in the species (Mary-Anne Lea, unpublished data).

Aims

Information on the foraging ecology and habitat use of higher-trophic predators is central to understanding their role in the changing Southern Ocean ecosystem and to inform management decisions. By examining inter-relationships across ecological levels, a broader understanding of a species' biology in the context of this environment can be realised.

The overarching aim of this thesis was to quantify the habitat use, foraging behaviours and the drivers of these for female Antarctic fur seals during the poorly studied non-breeding winter period, from the individual to the species level. Being an abundant and major consumer in the Southern Ocean with a wide-ranging unconstrained distribution, this species is particularly well suited to such an examination. The main objectives were achieved mostly through the deployment of global-location sensing (GLS) loggers to provide information on the at-sea foraging movements of female fur seals as part of large-scale tracking program. This work was conducted at three circumpolar breeding colonies: Marion Island (Prince Edward Islands), Bird Island (South Georgia) and Cape Shirreff (South Shetland Islands) between the years 2008 to 2013. The thesis is organised into four research chapters, each addressing a key objective, and one chapter drawing them together in a general discussion. A brief outline for each chapter and associated objectives is presented below.

Chapter 2 – *Individual foraging site fidelity*

- Main objective: Ascertain the degree of foraging site fidelity.

Location information from Marion and Bird Island female Antarctic fur seals was used to quantify the fidelity of individuals within and across years to at-sea foraging sites over four years. Data from seals which undertook multiple foraging trips over the course of the winter were used to assess within-year foraging site fidelity, while the movements of those animals tracked across multiple years were used to examine between-year foraging site fidelity. The environmental conditions of areas of re-use were revealed and the ecological and evolutionary context for these behaviours was considered.

Chapter 3 – *Dive behaviour and foraging strategies*

- Main objective: Identify major foraging strategies and associated costs and benefits.

By combining location estimates with horizontal movement data from time-depth recorders (TDRs) the diving behaviour and vertical habitat use of Antarctic fur seals from Marion Island was examined during their post-breeding migrations for the first time. A novel broken-stick analysis was used to measure within-dive foraging effort and identify divergent foraging strategies across a wide geographic area. The costs and benefits associated with the observed behavioural choices were identified. The relationship between movement responses across horizontal and vertical dimensions was also assessed.

Chapter 4 – *Winter habitat use of populations*

- Main objective: Identify important winter foraging habitat and their associated environmental characteristics.

The spatial distribution patterns of Antarctic fur seals from three Southern Ocean colonies were examined during winter. Habitat models were constructed to examine the relationship between habitat use and the oceanic environment, revealing the key factors influencing foraging areas. Predictive models were interpolated across the spatial domain of each colony to identify core winter foraging habitats.

Chapter 5 – Environmental change and management considerations

- Main objective: Quantify change in winter habitat over recent decades and identify seasonal habitat use to facilitate assessment of the degree of overlap with Southern Ocean management areas and fisheries.

By expanding the habitat models developed in Chapter 4, the response of foraging female Antarctic fur seals to environmental change was assessed. Remotely sensed environmental data were used to reconstruct the historical foraging habitats of colonies and changes to habitats were quantified. Seasonal habitat models were developed to measure variation in habitat use across the winter to better understand the spatio-temporal overlap with Southern Ocean management areas and the potential for interactions with fisheries activities.

Thesis structure

This thesis has been written as a series of separate manuscripts. Consequently, there is some overlap of text and ideas between chapters. All chapters, with the exception of this introductory chapter and general discussion, consist of manuscripts that are either published papers, papers accepted for publication, or in preparation for submission. I was the senior author on each paper. Co-authors are listed with each chapter title and their contributions are detailed in the Statement of Co-authorship at the front of this thesis. A single bibliography is presented at the end of the thesis using the Functional Ecology referencing style.

Chapter 2

Return customers: Foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals

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Abstract

Strategies employed by wide-ranging foraging animals involve consideration of habitat quality and predictability and should maximise net energy gain. Fidelity to foraging sites is common in areas of high resource availability or where predictable changes in resource availability occur. However, if resource availability is heterogeneous or unpredictable, as it often is in marine environments, then habitat familiarity may also present ecological benefits to individuals. We examined the winter foraging distribution of female Antarctic fur seals, *Arctocephalus gazella,* over four years to assess the degree of foraging site fidelity at two scales; within and between years. On average, between-year fidelity was strong, with most individuals utilising more than half of their annual foraging home range over multiple years. However, fidelity was a bimodal strategy among individuals, with five out of eight animals recording between-year overlap values of greater than 50%, while three animals recorded values of less than 5%. High long-term variance in sea surface temperature, a potential proxy for elevated long-term productivity and prey availability, typified areas of overlap. Within-year foraging site fidelity was weak, indicating that successive trips over the winter target different geographic areas. We suggest that over a season, changes in prey availability are predictable enough for individuals to shift foraging area in response, with limited associated energetic costs. Conversely, over multiple years, the availability of prey resources is less spatially and temporally predictable, increasing the potential costs of shifting foraging area and favouring long-term site fidelity. In a dynamic and patchy environment, multi-year foraging site fidelity may confer a long-term energetic advantage to the individual. Such behaviours that operate at the individual level have evolutionary and ecological

implications and are potential drivers of niche specialization and modifiers of intra-specific competition.

Introduction

Foraging animals are expected to make prudent choices in order to minimise energy expenditure whilst maximising energy intake. The choice of foraging habitat is an important component of this, and various foraging ecology models have sought to describe how these choices might be made. One of the best established models, the Marginal Value theorem (Charnov 1976), predicts that foragers in patchy environments balance their rate of energy intake with the energy expenditure associated with travel, search and prey handling times, and that as energy intake in a particular area declines, foragers should move to other, more profitable areas. While various studies of foraging ecology yield support for such theories (Cowie 1977; Morris & Davidson 2000; Boivin *et al.* 2004), other descriptions of foraging behaviours apparently seem contradictory. Site fidelity; the return to and re-use of a previously occupied area (Switzer 1993), where reduced patch switching often results, is one such example. Individuals from a range of taxa including mammals (Rydell 1989; Schaefer *et al.* 2000), birds (Latta & Faaborg 2001; Coleman *et al.* 2005), fish (Verweij & Nagelkerken 2007) and insects (Fresneau 1985) repeatedly return to foraging sites. We may consider such behaviour a form of optimal foraging (MacArthur & Pianka 1966), where the act of remaining faithful to a site delivers an increase in net energy intake, particularly in environments with high resource availability.

The quality of resources, however, is unlikely to be the only factor influencing an animal's choice of foraging habitat, with the stability and predictability of the resources also likely to play an important role. When habitats are relatively stable, or have predictable spatial and temporal changes in food availability, site fidelity can occur (Andersson 1980). This is particularly common in terrestrial environments with highly predictable food resources, such as fruiting or flowering trees (Markus & Hall 2004). However, foraging site fidelity is also documented in marine species, including seabirds (Irons 1998), pinnipeds (Stewart & DeLong 1995; Call *et al.* 2008), turtles (Avens *et al.* 2003) and cetaceans (Calambokidis *et al.* 2001), which typically rely on what are regarded as unpredictable and patchily distributed prey (Weimerskirch 2007; Benoit-Bird *et al.* 2013). If habitat quality is heterogeneous and unpredictable, either spatially or temporally, site fidelity can also present ecological benefits to individuals, such as familiarity with resources (Greenwood 1980) or reduced predation risk (Stamps 1995). For long-lived animals, such as many vertebrate marine predators, the persistence of long-term fidelity (i.e. over months and years) to foraging sites (Trathan *et al.* 1998; Trathan *et al.* 2006) may serve to maximise net energy intake over the individual's lifetime (Perry & Pianka 1997), even if energy intake is not high in all years (Bradshaw *et al.* 2004b).

The availability of prey resources to marine predators varies through normal atmospheric and oceanic processes, for example in the Southern Ocean, the Southern Annular Mode (SAM) (Forcada & Trathan 2009), the El Niño Southern Oscillation (ENSO) and the formation and retreat of sea ice (Murphy *et al.* 2007). Despite this, just how higher trophic levels will respond to future change remains poorly understood. This is especially important for animals demonstrating strong site fidelity as it raises questions about behavioural plasticity and their ability to respond to future habitat alterations such as those arising from the effects of climate change and the activities of fisheries. Typically, ecologists have viewed foraging behaviour at the population level, treating individuals as ecologically alike (Cam *et al.* 2002). However, it is at the individual level where natural selection operates and, consequently, individual specializations have potential evolutionary (e.g. niche specialization) and ecological (e.g. intra-specific competition) implications for population structure. To reliably assess the importance of behaviours such as individual site fidelity, longitudinal studies are required. Few such studies exist for marine predators, with only a handful seeking to track the same individuals over multiple seasons within the same area (Bradshaw *et al.* 2004b; Broderick *et al.* 2007; Chilvers 2008; Schofield *et al.* 2010; Augé *et al.* 2013).

Antarctic fur seals (*Arctocephalus gazella*, AFS) are top marine predators that present an ideal model for investigating site fidelity. During the non-breeding austral winter many female AFS undertake wide-ranging migrations or dispersals (Boyd *et al.* 2002; Staniland *et al.* 2012). During this time, they are free from the constraints of central place foraging (Orians & Pearson 1979) associated with provisioning their offspring. These movements, therefore, afford insights into foraging habitat preferences during an unconstrained period. Furthermore, female AFS become pregnant during the winter season when the blastocyst implants (Boyd 1996) and must make judicious choices in regards to maximising their energy intake in the important pre-breeding period. Studies of the foraging behaviour of AFS during the summer breeding season are frequent in the literature and generally demonstrate that animals target specific foraging areas (Lea & Dubroca 2003; Staniland *et al.* 2004; Staniland *et al.* 2011); nevertheless, few data exist concerning the degree to which individuals return to these areas in successive trips (Bonadonna *et al.* 2001) and no studies have investigated longer term site fidelity over multiple seasons.

We quantified the winter foraging patterns of female AFS over four years between 2008-11 to identify the degree of site fidelity to Southern Ocean foraging habitats. A coordinated, long-term tracking program allowed us to examine site fidelity at two scales: within a year and between years. We examined site fidelity in relation to several remotely-sensed environmental parameters, using long-term oceanic variability (i.e. predictability) as a proxy for productivity and prey availability (Guinet *et al.* 2001; Bradshaw *et al.* 2004b). We hypothesise that fidelity to foraging areas will be related to resource availability and that this behaviour will confer energetic benefits to the individual. We discuss the possible mechanisms driving foraging site fidelity and the potential ecological and evolutionary implications of this behaviour.

Methods

ETHICS STATEMENT

All animal handling and experimentation were undertaken with approval from the University of Tasmania Animal Ethics Committee (permit A001134), the University of Pretoria Animal Use and Care Committee (permit AUCC 040827-024) and the joint British Antarctic Survey-Cambridge University Animal Ethics Review Committee (does not issue permit numbers). Considering the very small size of the tags used in this study (see below) and the relatively high rate of recovery at Marion Island (Table 2.1), the impact of animals in carrying these tags is minimal.

Table 2.1. Sample sizes (number of individual animals and trips) by site and year used to estimate foraging habitat overlap at two temporal scales, within-year (encompasses multiple foraging trips undertaken by an animal in one season) and between-year (animals tracked over multiple years). Between-year fidelity (YES or NO) indicates for which years multi-year animals were tracked with the number of individuals in each of those years in brackets.

Site	**Year**	**GLS model**	**GLS deployed**	**GLS recovered**	**Animals tracked**		**Trips available**[a]		
					Fidelity level		All	Fidelity level	
					Within-year	Between-year[b]		Within-year	Between-year
Marion Island	2008	Mk7	30	20	9	Yes (7)	42	4	18
	2009	Mk7	31	15	8	Yes (7)	25	10	17
	2010	Mk5, 7 & 19	16	9	3	Yes (1)	17	14	4
	2011	Mk7 & 19	42	31	19	Yes (4)	71	2	7
	All years		119	75	39	8	155	30	46
Bird Island	2008	Mk7	29	3	2	No	6	24	-
	2009	Mk7	30	9	5	No	18	15	-
	2010	Mk7 & 19	30	10	5	No	21	9	-
	2011	Mk 19	30	6	4	No	11	46	-
	All years		119	28	16	No	56	94	-
Total			**238**	**103**	**55**	**8**	**211**	**124**	**46**

[a]Refers to all trips that were undertaken by tracked animals (All), and the number of trips that could be used to compute utilisation distributions based on suitable minimum number of ARS locations (Fidelity level: within-year and between-year, see results).

[b]Between-year fidelity (YES or NO) indicates for which years multi-year animals were tracked with the number of individuals in each of those years in brackets.

STUDY SITE, ANIMAL HANDLING AND INSTRUMENTATION

The study took place on Marion Island (46°54'S, 37°44'E), Prince Edward Islands, southern Indian Ocean and Bird Island (54°00'S, 38°03'W), South Georgia, southern Atlantic Ocean between 2008 and 2011 (Fig. 2.1). Breeding adult female AFS were captured during the latter part of lactation (February to April) after they had dispersed from breeding harems. On restraint, individuals were instrumented with global location sensing (GLS) loggers to track at-sea position during their winter migrations (~8-9 months from April to December). Coloured plastic flipper tags (Dalton Supplies, Henley-on-Thames, UK) bearing a matching unique numeric sequence were inserted into the trailing edge of each fore-flipper (Staniland *et al.* 2012). The GLS loggers were first attached to a metal flipper tag using a two-part epoxy (Araldite K268, Ciba-Geigy Corp., Basel, Switzerland) and a plastic cable tie; this was then deployed on the fore flipper paired with one of the plastic flipper tags. Three models of GLS loggers manufactured by the British Antarctic Survey (BAS, Cambridge, UK) were deployed during the four-year study (Mk5 and Mk7 – 18 x 18 x 6.5 mm, 3.6 g and Mk19 – 16 x 14 x 6 mm, 2.5 g) (Table 2.1).

Seals were recaptured and their GLS loggers recovered at the beginning of the following austral summer (November to December) when pregnant females return to the colony to pup. Five animals were not recaptured until the end of the following winter and three individuals were tracked over three years (Table 2.2). As this study did not form part of a wider demographic enquiry, the age and reproductive success of tracked animals is unknown.

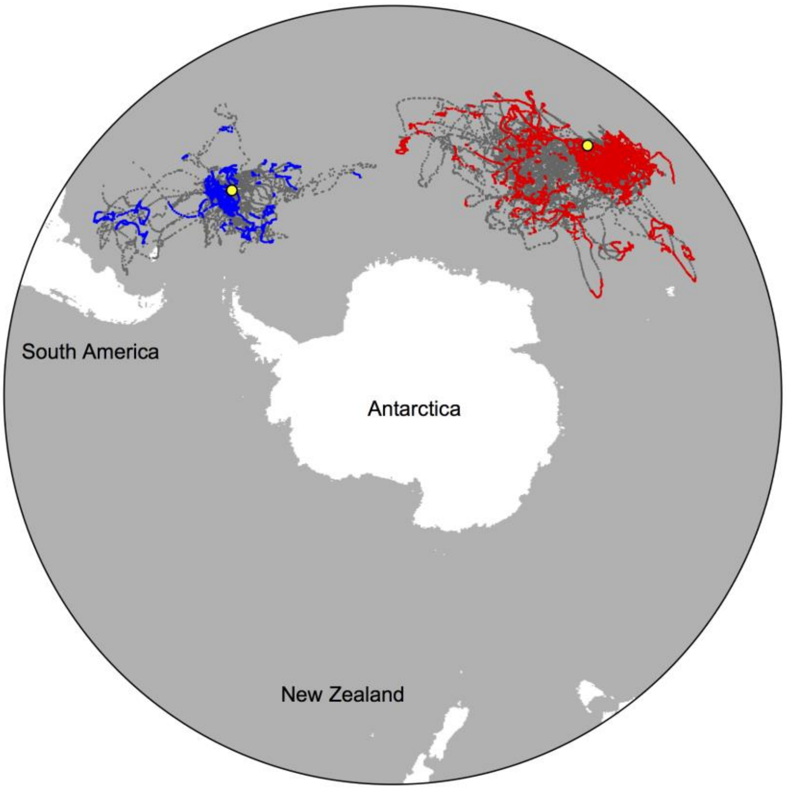

Figure 2.1. Mean estimated winter migrations for 59 adult female Antarctic fur seals from Bird Island and Marion Island, 2008-11. Locations in red and blue represent likely area-restricted search (ARS) behaviour for animals from Marion and Bird Island respectively, inferred through state space modelling. Colonies are shown in yellow.

The loggers measured ambient light every minute and recorded the maximum value for every 10-minute period (5 minutes for Mk19 units). They also recorded sea temperature after 20 minutes continuous wet, repeated every 4 - 24.8 hours, and reset anytime the unit was dry for >3 - 6 seconds. Temperature was logged at a resolution of 0.125°C and with accuracy of ± 0.5°C, which was later improved by temperature calibration of each tag in a water bath (Lea *et al.* In review). The light loggers on each device were calibrated at each study site for approximately 5-7 days either immediately before or after deployment to obtain a solar elevation curve at a known locality, which was necessary for location estimation.

Table 2.2. Foraging trips per year and utilisation distribution overlap values (Bhattacharyya's affinity) for eight female Antarctic fur seals from Marion Island that were tracked for multiple winters between 2008-2011.

Seal ID	Year				Total trips	Within year overlap[a]	Between year overlap
	2008	2009	2010	2011			
PP620	1	1	-	-	2	-	0.05
PP623	2	2	-	3	7	0.21	0.80
WB438	9	6	-	-	15	0.24	0.67
WB449	1	3	-	1	5	0.20	0.52
WB458	1	2	-	-	3	-	0.02
WB462	-	1	-	2	3	-	0.84
WB482	1	-	-	1	2	-	0.04
WW422	3	2	4	-	9	0.13	0.81
	2.6 ± 1.1	2.4 ± 0.6	-	1.8 ± 0.5	5.8 ± 1.6	0.2 ± 0.02	0.50 ± 0.08

[a]Animals with no within year overlap value either undertook only one trip per year, or successive trips were excluded from analyses as they contained fewer than 10 ARS locations (see Methods).

LOCATION ESTIMATION

Location estimates were produced from the raw light and temperature data using the Bayesian approach of Sumner et al. (2009) using the R package 'tripEstimation' (Sumner & Wotherspoon 2010) following the methodology detailed in Lea et al. (In review) (Supporting Information S2). In brief, the posterior mean for each twilight period (dawn and dusk) were summarized based on the accepted Markov Chain Monte Carlo (MCMC) samples, resulting in two location estimates per day. The accuracy of location estimates using this approach is shown to be 70 ± 35 km for an AFS carrying GLS and Argos tags simultaneously. (Lea *et al.* In review). Mean location estimates were used to facilitate the calculation of utilisation distributions (UD, see below), which would otherwise be computationally restricted if all MCMC estimates were considered. To ensure that UDs, and subsequent overlap, were not affected by this approach, a comparison was made with UDs calculated from a fixed number of accepted MCMC samples for a subset of animals (Protocol S1).

Furthermore, our state-space modelling approach also necessitated mean location estimates. State-space models built specifically for geolocation data were used to infer area restricted search (ARS) behaviour, indicative of probable large-scale foraging behaviour (Patterson *et al.* 2008). Model design and implementation closely followed the framework proposed by Jonsen *et al.* (2005) and is described in detail in Lea et al. (In review) (Supporting Information S2).

Individual trips were identified by examining the raw light data, with on-shore periods typified by obvious messy light curves caused by the animal periodically shading the light sensor during haul out. Each trip was analysed independently. Winter foraging trips were considered to be from the first post-weaning excursion (typified by a clear increase in trip duration when compared with shorter trips during lactation), to the return of the animal to the colony the following breeding season.

UTILISATION DISTRIBUTION ESTIMATION AND OVERLAP

To assess habitat use, and the potential for overlap during winter foraging trips we calculated the 95% UD using the fixed Kernel Density Estimation method derived from the least-squares cross validation bandwidth (Seaman & Powell 1996) in the R package ‘adehabitatHR’ (Calenge 2013). Only locations associated with ARS behaviour, as indicated by the state-space models, were included in the analyses, meaning UDs represented an individual’s broad-scale foraging range rather than whether individuals simply followed the same migratory pathways. We computed the UD for individual animals to assess site fidelity at two scales: between years and within years (see Table 2.1):

1. *Between year site fidelity* - the UD was computed using all the ARS locations obtained for each year for those animals tracked over multiple winters.

2. *Within year site fidelity* – this was examined by calculating the UD based on ARS locations of individual foraging trips undertaken by each animal during a single year.

For all analyses, short trips with fewer than 10 locations were excluded as kernel estimation is robust above a minimum threshold of locations (Börger *et al.* 2006). In some instances when UD models would not converge, a small amount of noise was introduced to location estimates using the "jitter" function (package 'base') to counter the high variance in estimates associated with spatially clustered locations (Silverman 1986) experienced for ARS locations. The amount of "jitter" introduced was never greater than the mean error surrounding the location estimates. Utilisation distributions were estimated across a 1° raster grid encompassing the area 80°00'S - 30°00'S; 140°00'W - 00°00'E, to aid subsequent comparison with environmental variables.

Fieberg and Kochanny (2005) undertook an extensive review of the indices of overlap between utilization distributions (UD), recommending Bhattacharyya's affinity (BA) (Bhattacharyya 1943) for a general measure of similarity between UD estimates. BA considers the spatial domain of home ranges, ignoring their density of use, and estimates the percentage overlap between them when overlaid. We determine this an appropriate method as the primary interest of this study is the outright re-use of previous areas, rather than a finer scale assessment of home ranges. BA is given as a measure of affinity ranging from 0 (no overlap) to 1 (identical UDs) and was calculated using the "kerneloverlaphr" function in the 'adehabitatHR' package (Calenge 2013).

For a three or more way overlap, all trips/years were included and any grid cells that were used more than twice were considered to be overlapping, regardless of the degree of overlap.

ENVIRONMENTAL VARIABILITY

To investigate the role of environmental characteristics in influencing the degree of UD overlap for AFS, we extracted sea surface temperature (SST), sea surface height anomaly (SSHa) and chlorophyll a concentration (CHLa), from regions corresponding to UDs (Table 2.3). All available data were used and then restricted to the period of winter migrations (April – December). We then calculated the mean and standard deviation (SD) of each parameter per pixel over the time period to create a temporal climatology (Sumner *et al.* 2003), permitting an assessment of the long-term temporal patterns of variability (Bradshaw *et al.* 2004b).

A comparison of environmental parameters within *non-overlapping areas* (cells used by an individual only once. i.e. year j for between-year fidelity, and trip j for within-year fidelity) and *overlapping areas* (grid cells used more than once i.e. year $j + 1$, and trip $j + 1$) was undertaken with logistic Generalised Linear Mixed Models (GLMMs) using the “lmer” function (package ‘lme4’). The response term (whether a grid cell was overlapping or non-overlapping) was fitted to a binomial error structure and logit-link function due to the binary nature of the response variable and the continuous nature of the predictor variables. Seal identity was included as a random effect when investigating between-year fidelity, whilst both seal identity and site were fitted as random effects when investigating within-year fidelity (all seals with multi-year tracks were from Marion Island, Table 2.1). Prior to model building, correlation between predictor variables was examined with a correlation matrix and

Pearson product-moment correlation analyses were undertaken to quantify co-linearity. The distribution of predictor variables was also examined and data were log-transformed to meet the assumptions of normality where appropriate. Models were fitted using Laplacian approximation, which is the estimation method in the ‘lme4’ package, and were built from the null model to the saturated model considering all possible model combinations. Models were ranked using the AIC (Akaike Information Criterion), which includes the maximized log-likelihood of the model and penalises model complexity (Johnson & Omland 2004). The best of the available models was determined using delta AIC and weights of evidence (Burnham & Anderson 2002).

Table 2.3. The remotely sensed data source, timespan, spatial and temporal resolution and whether temporal climatologies were calculated for oceanographic data for comparison between overlapping and non-overlapping foraging regions.

Variable	Source	Frequency	Spatial resolution[a]	Timespan	Variance
SST – sea surface temperature	NOAA Optimum Interpolation daily Sea Surface Temperature[b]	5 days	0.25 degree	1988-2011	Yes
SSHa – sea surface height anomaly	AVISO[c]	7 days	1/3 degree (Mercator)	1999-2011	Yes
CHLa – chlorophyll a concentration	MODIS[d]	8 days	0.1 degree	2002-2011	Yes

[a]All data were reprojected into 1 degree pixels
[b]OI-daily: http://www.ncdc.noaa.gov/oa/climate/research/sst/oi-daily.php
[c]AVISO: http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/index.html
[d]MODIS: http://oceancolor.gsfc.nasa.gov/

Results

LOCATION STATISTICS AND TRACK SUMMARIES

We collected winter tracks for 103 adult female AFS from Marion Island (n=75) (Lea *et al.* 2014a) and Bird Island (n=28) (Lea *et al.* 2014c) between 2008-11. Multi-year tracks were available for eight individuals, all from Marion Island (N=46 trips) and tracks of repeat trips within a year were available for 55 individuals (N=124 trips), totalling 211 individual foraging trips and 33 716 location estimates, of which 15 295 (45%) were identified as likely ARS behaviour (Fig. 2.1). Four individuals completed multiple within and between-year trips, meaning the total number of animals used for analyses was 59. A detailed summary of sample sizes across the colonies and years is given in Table 2.1. Henceforth, all means are reported plus or minus standard error and all t-tests are two tailed. Among all individuals tracked, the mean maximum distance travelled from the colony was 1259 ± 56 km per trip (range 104-4528 km). The mean foraging trip duration was 123 ± 6 days (range 6-266 days) and the mean proportion of the trip spent in area-restricted search (ARS) behaviour was 41 ± 2 % (range 1-96 %).

FORAGING SITE FIDELITY

To determine if foraging areas were unique to individual seals we compared the overlap of UDs across all animals at each site. The mean inter-individual overlap of foraging home ranges was 0.14 ± 0.01 (range 0.01-0.28) at Marion Island and 0.22 ± 0.03 (range 0.01-0.38) at Bird Island. This indicates that individuals from these populations forage over a broad geographical range and that the overlap of foraging home ranges reported here is not merely a product of all animals moving to the same general area.

WITHIN-YEAR FIDELITY

Thirteen trips were excluded from these analyses as they were either composed of fewer than 10 ARS locations, or would not converge during estimation of the UD. Therefore, 124 trips from 42 individuals were available, with individuals performing between two and nine repeat trips within a year. The mean size of UDs per trip was 23.4 ± 1.6 (range 4-136) 1° grid cells. There was no difference in the mean size of UDs of trips from Marion (22.7 ± 1.8) and Bird Island (25.6 ± 3.2; $t_{46} = -0.77$, $P = 0.445$). Within individuals, the mean overlap of the foraging home range between successive trips was 0.15 ± 0.02 (range 0-0.81) at Marion Island and 0.21 ± 0.05 (range 0-0.74) at Bird Island. Across the two colonies, the mean within-year overlap of individual foraging home ranges was 0.16 ± 0.02 (range 0-0.80; Fig. 2.2).

BETWEEN-YEAR FIDELITY

A total of 4138 ARS locations were available for eight individual animals tracked over multiple years. Individuals were tracked for either two or three seasons and undertook between one and nine trips per season (Table 2.2). The mean size of UDs was 50.3 ± 3.9 (range 22-92) 1° grid cells (Fig. 2.3). Within individuals, the mean home range overlap between years was 0.50 ± 0.08 (range 0.02-0.84; Fig. 2.4; Table 2.2). However, the degree of home range overlap within the sample population displayed an obvious bimodal distribution (Fig. 2.4), with three individuals having overlap values of 0.05 or less, while the five remaining individuals had overlaps of greater than 0.50 (Table 2.2). Overall, foraging home range overlap was significantly higher between years than within years, both when comparing across all animals ($t_{24} = 3.96$, $P < 0.001$) and animals from Marion Island only ($t_{23} = 4.04$, $P < 0.001$).

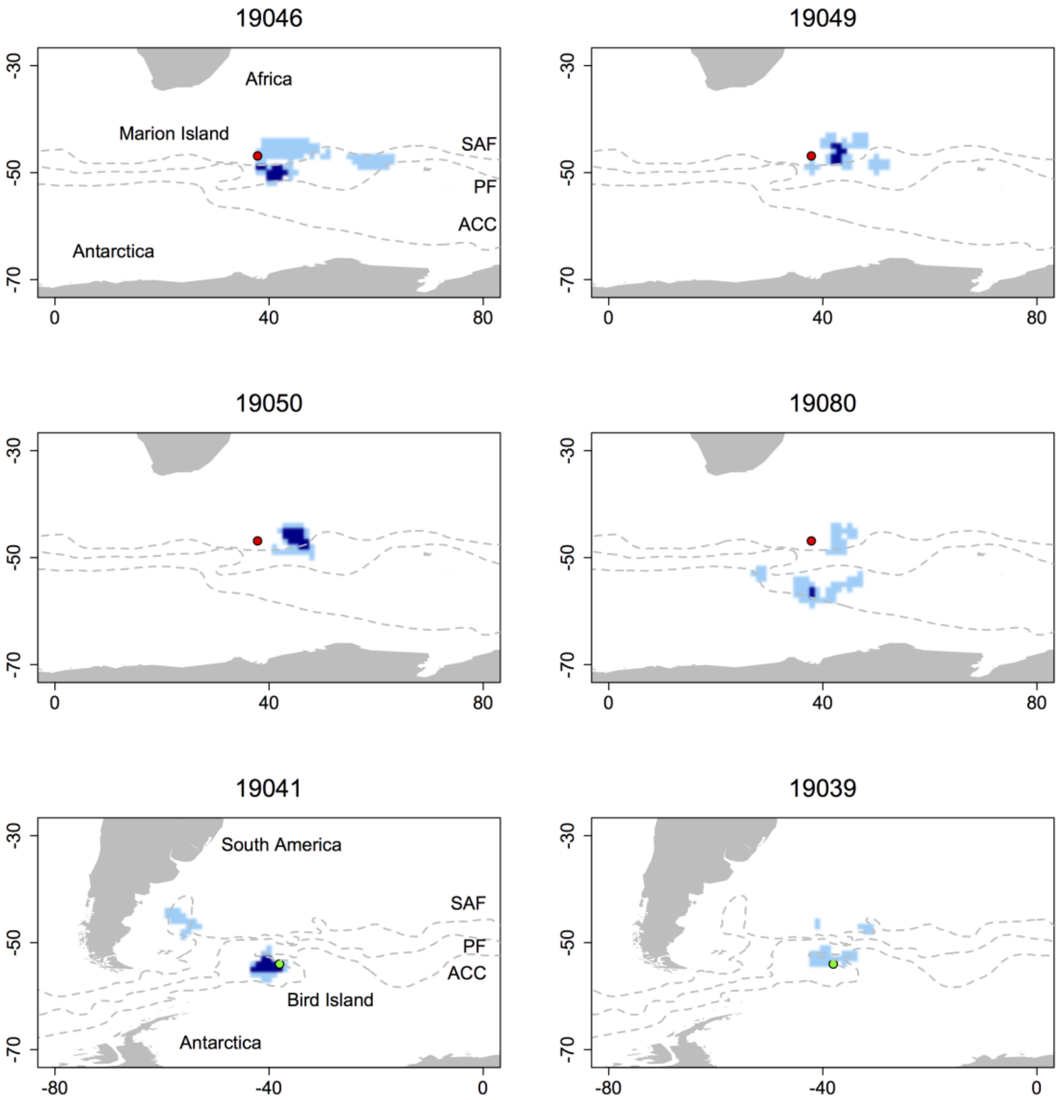

Figure 2.2. Within-year winter foraging habitat of six example adult female Antarctic fur seals. Light blue indicates area-restricted search (ARS) cells used during one trip only, while dark blue indicates overlapping cells used across multiple trips within a year. Lines indicate the mean location of the sub-Antarctic front (SAF), polar front (PF) and the Antarctic circumpolar current (ACC). Marion and Bird Island are shown in red and green respectively.

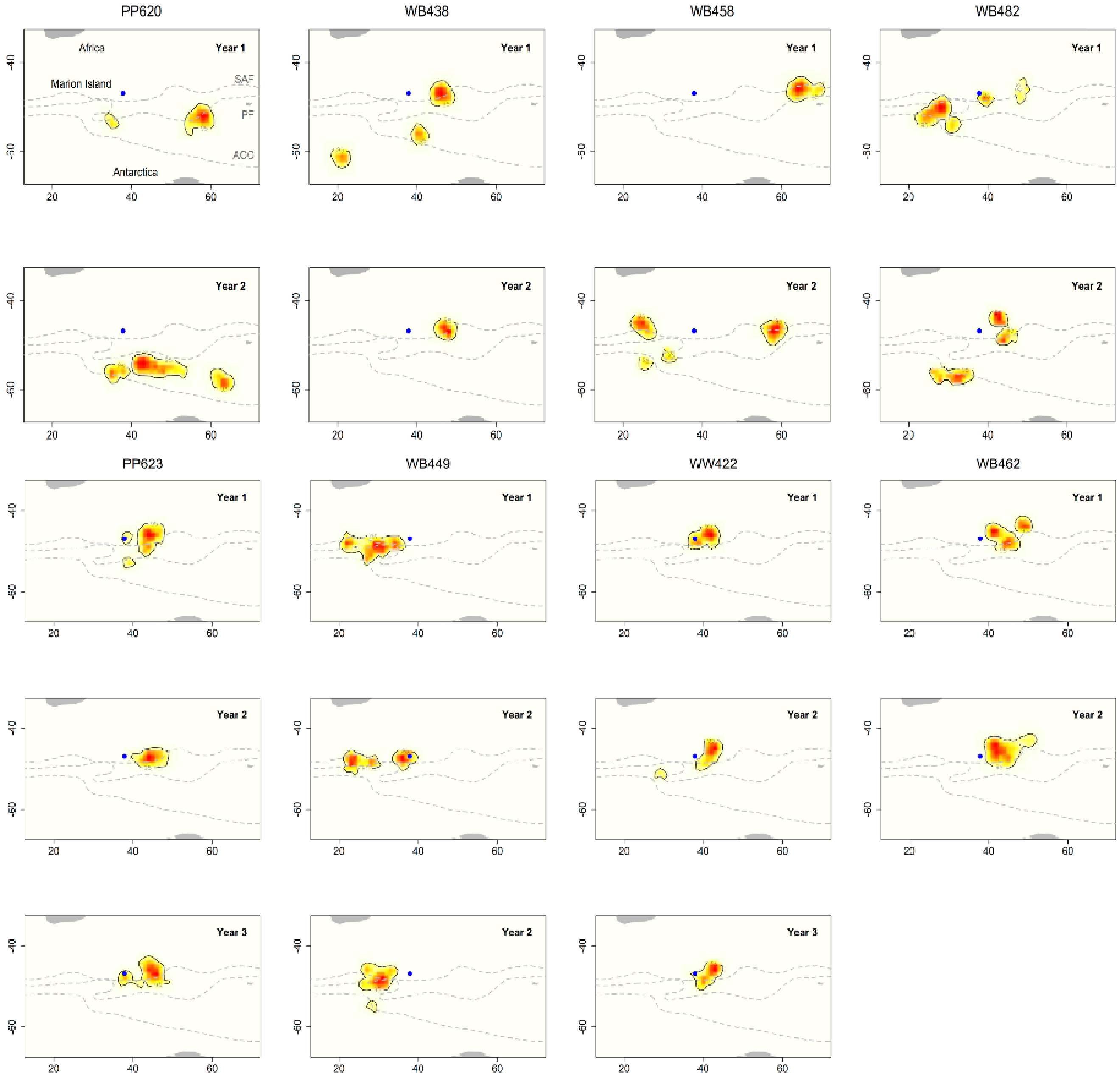

Figure 2.3. Utilisation distributions (UDs) for eight female Antarctic fur seals that were tracked over multiple winters. The black lines denote the 95% UD, which represents the annual foraging kernel home range of each animal. The individuals were tracked from Marion Island (blue circle) for either two or three years between 2008-2011. Grey lines show the mean position of the sub-Antarctic front (SAF), polar front (PF) and the Antarctic circumpolar current (ACC).

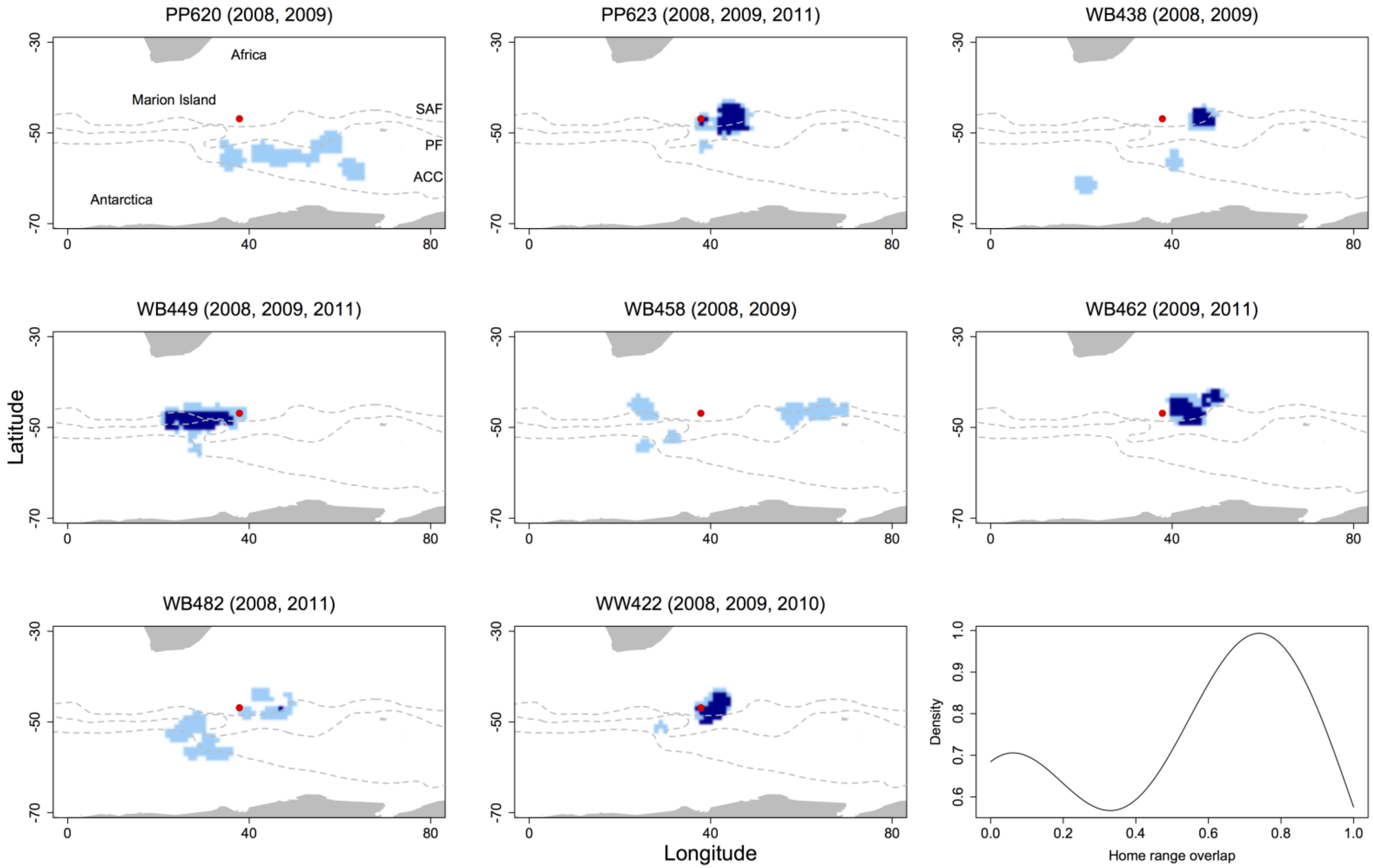

Figure 2.4. Multi-year foraging habitat use of eight female Antarctic fur seals from Marion Island during winter between 2008-2011. Light blue denotes cells used in one year, dark blue denotes overlapping cells used in multiple years. Lines indicate the mean location of the sub-Antarctic front (SAF), polar front (PF) and the Antarctic circumpolar current (ACC). The density distribution of home range overlap values (Bhattacharyya's affinity) is shown in the bottom right panel.

ENVIRONMENTAL CHARACTERISTICS OF HIGH USE REGIONS

We compared environmental characteristics of individual foraging home ranges within and outside the overlap areas. Satellite-derived oceanographic parameters (sea surface temperature (SST), sea surface height anomaly (SSHa) and chlorophyll a concentration (CHLa) (Table 2.3) of the home ranges were examined. All data were re-projected into raster grids with a 1° resolution and a spatial extent of 80°S-30°S, 140°W-80°E. SSHa data was interpolated from the original 1/3 degree Mercator resolution. The long-term mean and SD for the winter season for each grid cell over the region was calculated. After examination of these climatologies, we found there was poor temporal resolution of CHLa data during the winter period for many grid cells across the region, a common issue with satellite ocean colour products in the Southern Ocean caused by reduced temporal and spatial coverage corresponding to increased cloud cover at this time of year (Dragon *et al.* 2011). CHLa data was therefore excluded from further analyses to ensure all climatologies were calculated from a consistent minimum number of data points across the spatial domain.

REGIONS OF WITHIN-YEAR OVERLAP

We compared the environmental climatologies of regions of home range overlap between successive foraging trips within a year, with non-overlapping regions visited during one trip only. A Pearson product-moment correlation analysis indicated co-linearity between SST_mean and SST_SD ($r_{1335} = 0.58$, $P < 0.001$). SST_mean was therefore removed from the analyses as we were interested in the effects of long-term environmental variability on site fidelity and the SST_SD (a measure of variance) is a more relevant variable. The best model regarding whether a grid cell was overlapping or non-overlapping (termed '*celluse*' in the model) included SST_SD and SSHa_mean (AIC weight = 0.593; model 1 Table 2.4a). A subsequent test for an interaction effect between the fixed predicator terms by including this in the model resulted in a poorer model performance (**Δ**AIC = 1.2; model 2 Table 2.4a). Based on the accepted model (model 1) the probability that grid cells would overlap across successive trips within a particular year increased for cells with lower SST_SD and negative SSHa_mean (Table 2.5a, Fig. 2.5a).

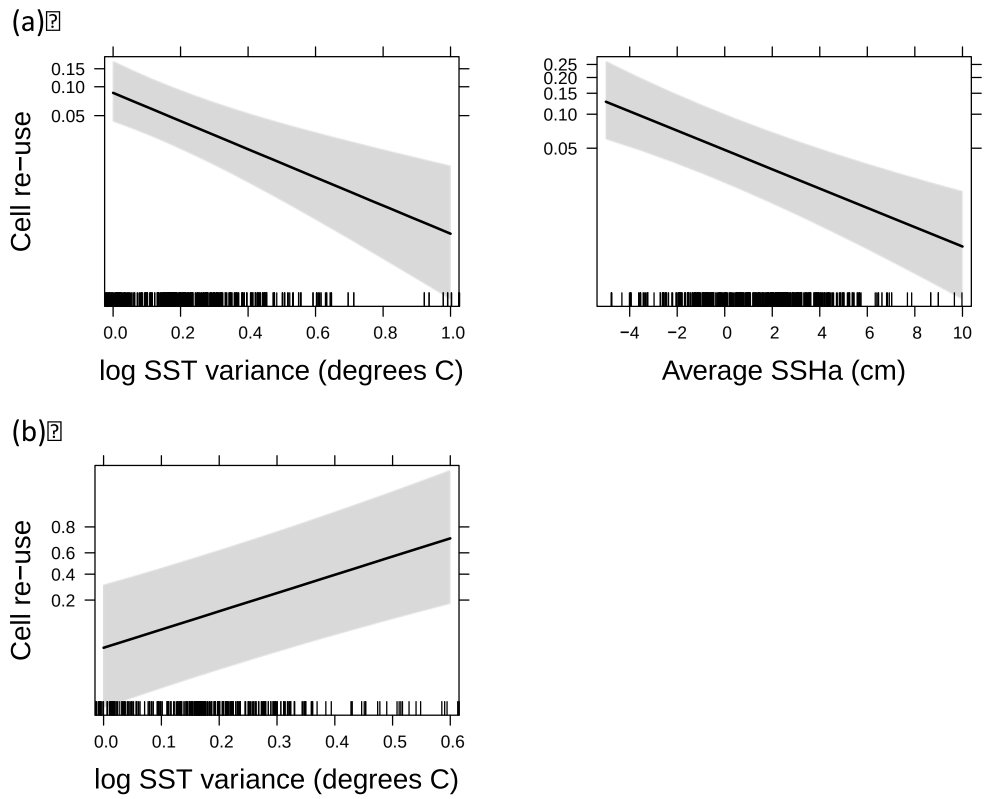

Figure 2.5. Probability of foraging site fidelity in relation to oceanographic parameters: (a) within a year and (b) between years. Curves were fitted using the best logistic GLMM respectively, as shown in Table 2.4. The grey bar represents the 95% confidence interval around the estimated effect.

Table 2.4. Summary of generalised linear mixed-effect model (GLMM) comparisons: (a) GLMMs of cell use for within-year fidelity include seal identity and site as random effects; and **(b)** GLMMS of cell use for between-year fidelity include seal identity as a random effect ("celluse" = overlapping or non-overlapping, SST_SD = sea surface temperature standard deviation, SSHa_mean = average sea surface height anomaly, SSHa_SD = sea surface height anomaly standard deviation). Only models with a delta AIC <10 are presented and the accepted model is presented in bold.

Candidate models	*k*	LL	AIC	**Δ**AIC	*w*AIC
(a) *GLMMs of oceanographic parameters – within year*					
1. celluse ~ SST_SD + SSHa_mean	**5**	**-413.8**	**837.7**	**0.0**	**0.593**
2. celluse ~ SST_SD + SSHa_mean + SST_SD*SSHa_mean	6	-413.4	838.8	1.2	0.331
3. celluse ~ SSHa_mean + SSHa_SD	5	-415.9	841.9	4.2	0.071
(b) *GLMMs of oceanographic parameters – between year*					
1. celluse ~ SST_SD	**3**	**-185.7**	**377.4**	**0.0**	**0.366**
2. celluse ~ SST_SD + SSHa_SD	4	-185.0	377.9	0.5	0.288
3. celluse ~ SST_SD + SSHa_mean	4	-185.3	378.6	1.2	0.202
4. celluse ~ SSHa_mean + SSHa_SD + SST_SD	5	-184.7	379.3	1.9	0.142

k, number of paramaters; LL, log-likelihood; AIC, Akaike's Information Criterion; **Δ**AIC, difference in AIC from that of the best fitting model; *w*AIC, AIC weight.

Table 2.5. Results for the best available generalized linear mixed-model (GLMM) examining the effects of log-transformed oceanographic parameters on **(a)** within-year foraging site fidelity and **(b)** between-year foraging site fidelity of female Antarctic fur seals. The best of the available models was determined using delta AIC and weights of evidence.

Parameter[a]	Variance	Estimate	SE	95% CI
(a) *Within-year*				
Fixed				
Intercept		-2.363	0.364	
SST_SD		-2.566	0.777	-4.09, -1.64
SSHa_mean		-0.211	0.045	-0.30, -0.12
Random				
Seal ID	3.078			
Site	0.000			
N_{cells} = 1337			N_{seals} = 42	
(b) *Between-year*				
Fixed				
Intercept		-3.187	1.188	
SST_SD		6.899	1.433	4.08, 9.71
Random				
Seal ID	9.753			
N_{cells} = 580			N_{seals} = 8	

[a]SST_SD, sea surface temperature standard deviation; SSHa_mean, average sea surface height anomaly; N_{cells}, number of grid cells; N_{seals}, number of individual seals; SE, standard error; 95% CI, 95% confidence interval.

REGIONS OF BETWEEN-YEAR OVERLAP

The environmental variables in regions of annual foraging home range overlap were compared with non-overlapping regions used in a single year only. The best model explaining cell overlap included SST_SD (AIC weight = 0.366; model 1 Table 2.4b). We found the probability that grid cells would overlap between years increased significantly for cells associated with higher variance in SST (Table 2.5b; Fig. 2.5b).

Discussion

Most studies of foraging behaviour seek to identify aspects of foraging strategies, such as habitat preference or prey searching techniques, with little consideration of whether particular strategies are consistent over time. It is often unknown if behaviours observed in one time period (i.e. one season or one foraging trip) are an accurate representation of an individual's longer-term foraging behaviour. This is true of many animal tracking studies, where we often do not know if locations from one year are indicative of a stable, long-term foraging strategy (Chilvers 2008). As foraging behaviour can vary in response to a multitude of factors including prey availability and distribution, environmental conditions, competition and the energetic requirements associated with age and breeding status (Boyd *et al.* 1994; Georges *et al.* 2000; Lea *et al.* 2002b; Bailleul *et al.* 2005; Field *et al.* 2005), it is important to identify the time-scale over which these behaviours persist. Our results showed that female AFS utilise a wide range of foraging habitats during the non-breeding winter season, with high levels of individual variation in foraging area as indicated by relatively low inter-individual foraging range overlap. Most individuals, however, displayed some degree of site fidelity to foraging areas, particularly over the mid to long term (i.e. between years).

When estimating the overlap of individual foraging areas the choice of scale will inevitably affect the results. Too fine a scale may yield little or no overlap, while high levels of overlap may result at coarser scales. Assessing the overlap of UDs, which provide a practical summary of space use for a given individual (Fieberg & Kochanny 2005), overcomes these issues. We calculated UDs across a 1° grid, chosen to aid comparison with environmental data and match the error uncertainty surrounding location estimates via geolocation (70 ± 35 km) (Lea *et al.* In review). As kernel density estimates are largely unaffected by grid size (Silverman 1986), the resolution of this grid does not have a significant impact on the estimates of UDs and their resulting overlap. The estimation of kernel based UDs are less accurate for small samples (Hoenner *et al.* 2012) and it is therefore possible that the lower overlap values reported within years are partly an artefact of fewer foraging locations from shorter trips. However, by excluding very short foraging trips (<10 ARS locations) from our analyses we are confident that our results are spatially robust.

Female AFS displayed strong individual foraging site fidelity between years. On average, seals utilised 50% (± 8% SE) of their overall foraging range across multiple years. Multi-year foraging site fidelity has been reported for few marine taxa including turtles (Broderick *et al.* 2007; Schofield *et al.* 2010) and rays (Dewar *et al.* 2008) and has also been noted in cetaceans mostly through re-sight studies (Calambokidis *et al.* 2001; McSweeney *et al.* 2007). Multi-year fidelity to foraging sites has been described in only a handful of pinniped species. Both Chilvers (2008) and Augé *et al.* (2013) showed that individual female New Zealand sea lions (*Phocarctos hookeri*) displayed strong site fidelity across two years, with, on average a 64% inter-annual overlap of home ranges during short autumn trips (Augé *et al.* 2013). Bradshaw *et al.* (2004b) also reported strong overlap in the habitat use of female southern elephant seals (*Mirounga leonina*) during post lactation (66%) and post moult (53%) trips from Macquarie Island. Using a different approach, Lowther *et al.* (2011) report broad scale multi-year site fidelity in Australian sea lions (*Neophoca cinerea*) using stable isotope analysis, with individuals consistently exploiting either inshore or offshore sites. Unlike New Zealand and Australian sea lions, which are typically benthic foragers that undertake short, repeat trips of several hundred kilometres (Augé *et al.* 2013), AFS (and southern elephant seals) can undertake wide-ranging foraging migrations of many thousands of kilometres (Boyd *et al.* 2002; Staniland *et al.* 2012). During this time, animals are exposed to a range of environmental conditions and are likely to be making judicious choices regarding foraging habitat selection. The eight animals tracked over multiple years in this study displayed a range of overlap values, with less than 5% overlap between years for three individuals, while five individuals recorded overlap values of greater than 50%, suggesting a bimodal strategy of foraging site fidelity among individuals. Precisely what drives these different strategies is difficult to say. However, we note that all animals displaying a low degree of site fidelity undertook a single foraging trip in each year, while animals that were highly faithful to foraging sites undertook at least two repeat trips throughout the years they were tracked.

We show that areas of multi-year overlap were not stable, but rather highly variable. Individual AFS that were tracked over multiple years displayed greater fidelity to areas characterised by a high variance in SST over multiple decades, with the probability that a cell would be used in multiple years higher for cells that exhibited greater long-term variability in SST, a potential proxy for long-term productivity. This is similar to southern elephant seals (Bradshaw *et al.* 2004b), which also returned to regions with higher long-term variance in SST, perhaps because these areas yield a higher prey abundance. Indeed the greater variability of SST within frontal regions of the Southern Ocean is often correlated with elevated productivity when compared with surrounding areas (Moore & Abbott 2002). We may consider such areas to be of higher habitat quality and, therefore, the target of foraging animals. While there is some degree of spatial predictability in the structure of major frontal regions in the Southern Ocean (Lutjeharms & Valentine 1984; Budillon & Rintoul 2003), the position of fronts varies between years (Sokolov & Rintoul 2002), making habitat quality less spatially and temporally predictable. Based on our sample size of eight seals, some individuals foraging in such variable environments appear to settle on a territory over the long-term. As an hypothesis for further study we suggest that this strategy will function to maximise net energy gain, and therefore fitness, over the long-term i.e. the individual's lifetime (Perry & Pianka 1997) and will seemingly persist regardless of annual variations in energy intake. The wide geographical spread of areas of foraging overlap observed among individuals indicates that these results are not simply a product of all individuals targeting the same broad areas and that longer-term fidelity to foraging regions is a more prevalent behavioural mechanism than offsetting changing prey resources by shifting to alternate foraging habitats.

Within an annual cycle, fidelity to foraging sites was much weaker with, on average, 16% (± 2% SE) of an individual's foraging area utilised across multiple trips. A similar level of intra-annual site fidelity (13% overlap) was reported in the foraging routes of lactating New Zealand fur seals (*A. forsteri*) (Baylis *et al.* 2012), while others have suggested greater intra-annual site fidelity in pinnipeds (Robson *et al.* 2004; Call *et al.* 2008), including AFS (Bonadonna *et al.* 2001). These studies, however, focussed on lactating females which have short, constrained foraging trips compared with the winter migrations reported here, and were based on directional fidelity rather than overlap of the individual's total foraging range, which are likely to produce greater estimates of fidelity. Using this method, Bonadonna *et al.* (2001) concluded that individual AFS learn the broad direction of travel to a profitable area, but during a trip they forage opportunistically whenever good patches are encountered. While seals may exploit areas of previous foraging success during subsequent trips, Staniland *et al.* (2004) suggest this occurs when patches are stable both spatially and temporally. The weaker foraging site fidelity within years reported in this study supports these findings and may be driven, in part, by seasonal shifts in ocean conditions. The results of the best-fit GLMM indicated that non-overlapping areas that were visited during one trip only, which was the dominant within-year strategy, were typified by high variability in SST. The habitat quality of these areas is likely to be less stable when compared with areas of low variance, yet may be associated with increased foraging habitat quality at particular times of the year.

We suggest that individual AFS display directional fidelity towards profitable regions within a year, as proposed by Bonadonna *et al.* (2001), on a broad to meso-scale, where they search for prey that are ephemeral at short-term temporal scales, which drives increased habitat switching. The 'win stay/lose switch' rule (Shields *et al.* 1988) seems applicable, where individual AFS will show greater fidelity if more successful during previous trips, but once success decays, presumably driven by a reduction in habitat quality with changing environmental conditions, animals wont return and instead search for more profitable areas. This strategy agrees with classic foraging ecology models such as the Marginal Value theorem (Charnov 1976), explaining how an individual will forage in a predictably patchy environment. It is difficult to infer what oceanic features the individuals adopting this strategy are targeting (if any), however, areas visited on one trip only were characterised by positive SSH anomalies. Such conditions may be indicative of short-lived meso-scale, warm-core eddy features (Ansorge & Lutjeharms 2005) which are associated with enhanced phytoplankton productivity (Dower & Lucas 1993) and known to be the target of foraging marine predators (Cottin *et al.* 2012), specifically from Marion Island (Nel *et al.* 2001).

There may be several benefits to those individual AFS that favour foraging site fidelity as a strategy, particularly over the long-term. Ultimately, it is a behavioural adaptation, involving consideration of both prey richness and predictability, which should minimise energy expenditure while maximising net energy gain. The underlying driver of this benefit may be rooted in spatial familiarity, where prior knowledge of an area leads to heightened individual fitness because of increased foraging effectiveness (Wolf *et al.* 2009), reduced predation risk and/or reduced travel costs (Stamps 1995). Furthermore, foraging site fidelity will probably strengthen with age, as there will be fewer reproductive events available to compensate for the potential costs associated with switching habitat (Switzer 1993). Authier *et al.* (2012) showed that a stable foraging strategy developed earlier in life corresponded with increased longevity in male southern elephant seals. The development of foraging site fidelity in AFS may be the result of initial success as a juvenile, where the productive foraging routes learned during early foraging trips (McConnell *et al.* 2002) persist into adulthood. Ideally, we would quantify the success of foraging site fidelity as a behavioural adaptation through demographic measures such as longevity or breeding success. Behavioural strategies that operate at the individual level, such as fidelity to foraging sites, have evolutionary and ecological implications and are potential drivers of niche specialization and intra-specific competition (Bolnick *et al.* 2003). Furthermore, the strong multi-year site fidelity demonstrated in this study raises questions about the ability of long-lived animals such as pinnipeds, to alter their habitat use in response to future environmental change.

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Supporting Information

Protocol S1. Effects of the Bayesian location estimation procedure on Utilisation Distributions and subsequent overlap.

To ensure that the Bayesian location estimation approach did not impact the degree of overlap of UDs (i.e. foraging home ranges) we undertook a comparison between our approach (summarizing the Markov Chain Monte Carlo (MCMC) samples to obtain a posterior mean) and using a fixed number of accepted MCMC samples for each twilight. We generated UDs from the ARS locations and compared their overlap between these two approaches for a subset of eight animals, all of which undertook multiple foraging trips.

Using our original approach, the mean within individual overlap for these animals was 0.14 ± 0.03 SE (range 0-0.23). In our comparison, for each ARS location estimate we re-imposed 200 points regularly sampled from the MCMC approximations. These inflated location estimates were then used to generate UDs for overlap comparison, which is a computationally intensive process and not practical for the full data set. In this instance, the mean within individual overlap was 0.13 ± 0.03 SE (range 0-0.22). There was no significant difference in the overlap of foraging home ranges between these two approaches ($t_7 = 1.27$, $P = 0.252$).

Supporting Information S2. Methods section of Lea et al. (In review) detailing the location estimation and state-space modelling procedures employed.

MOVEMENT MODELS

Geo-location models

Two location estimates per day (dawn and dusk) were generated from the raw light and temperature GLS data using the Bayesian approach of Sumner *et al.* (2009) based on the 'solar.model' example function in the R package '`tripEstimation`' (Sumner & Wotherspoon 2010).

A prior maximum extent was applied for each study area, 0° to 80° E, 70° to 30° S for Marion Island and 140°W to 10°E, 80° to 30°S for Cape Shirreff and Bird Island. Median daily temperatures measured by the GLS tag were compared to the NCEP 2 Reynolds Optimally Interpolated Sea Surface Temperature (SST) data to further restrict the allowable extent for each twilight period.

Each model initially specified a known release and recapture point and a movement model to constrain successive locations against a distribution of likely speed based on published Argos tracks for Northern fur seal females (Ream *et al.* 2005) which are similar in size and life history to Antarctic fur seals (Gentry & Kooyman 1986). The movement model distribution was lognormal with mean value 0.635 ± 0.509 (SD) kmh^{-1}. The release and recapture points were 46.875˚S 37.85˚E for Marion Island, 62.450˚S 60.783˚W for Cape Shirreff, and 54.00˚S 38.05˚W for Bird Island. In one instance the recapture point in intervening trips was removed when it was evident the seal had hauled out at another site.

The posterior for each model was approximated by Markov Chain Monte Carlo (MCMC) using the function 'metropolis' in the '`tripEstimation`' package (Sumner & Wotherspoon 2010). Each chain was run for 160,000 iterations and the first 10,000 were discarded to allow for model stability and convergence. Posterior mean and standard deviations for each twilight, were summarized directly based on the accepted MCMC samples.

Behavioural state models

To estimate the unobserved behavioural states of each seal, we used a hierarchical hidden Markov model (HMM; e.g., (Morales *et al.* 2004; Patterson *et al.* 2009)) fit to travel rates calculated between location estimates obtained via the `tripEstimation` R package (Sumner *et al.* 2009). The HMM classifies movement into two behavioural states, fast or slow movement, based solely on travel rate (Jonsen *et al.* 2005). Travel rates were modelled as realizations from two exponential distributions, corresponding to the two behavioural states:

$$r_{i,t} = \mathrm{Exp}(\lambda_{i,b_t}) \qquad (1),$$

where $r_{i,t}$ is the travel rate for the ith seal at time t and λ_{i,b_t} is the Exponential rate parameter ($1/\mathrm{E}[r_{i,t}]$) for the ith seal in behavioural state $b_t \in \{1, 2\}$. Switching between the behavioural states is treated as a Markov process with four possible transitions (switching from one state to the other and remaining in the current state) that yields the following conditional probability:

$$\begin{aligned}\phi_{i,1} &= \mathrm{P}(b_t = 1 | b_{t-1} = 1, \lambda_{i,1}, \lambda_{i,2}) \\ \phi_{i,2} &= \mathrm{P}(b_t = 1 | b_{t-1} = 2, \lambda_{i,1}, \lambda_{i,2})\end{aligned} \qquad (2),$$

where $\varphi_{i,1}$ and $\varphi_{i,2}$ are the switching probabilities associated with remaining in the fast movement state ($b_t = 1$) and switching from the slow movement state ($b_t = 2$) to the fast state, respectively. The other 2 possible transitions are the complements of (2). These probabilities were used to estimate b_t as a draw from a Bernoulli distribution (note that b_t is both the latent variable and the parameter index for the switching probabilities):

$$b_t = \mathrm{Bern}(\phi_{i,b_{t-1}}) \qquad (3).$$

Implementation of this HMM as a hierarchical model fit to multiple seals is straightforward under the Bayesian paradigm, using Markov chain Monte Carlo (MCMC) estimation tools provided by the software WinBUGS (Lunn *et al.* 2000). The hierarchical formulation assumes that both the rate parameters $\lambda_{i,1}$ and $\lambda_{i,2}$ and the switching probabilities $\varphi_{i,1}$ and $\varphi_{i,2}$, which are estimated for each seal, are realizations from distributions common to all seals. The common λ_1 and λ_2 distributions account for variability in travel rates among seals and the common φ_1 and φ_2 distributions account for variability in switching probabilities among seals. To facilitate estimation at both the individual and among-individual levels of this hierarchical structure, we used Beta-distributed priors on the individual switching probabilities $\varphi_{i,1}$ and $\varphi_{i,2}$ and half-Normal priors on the individual rate parameters $\lambda_{i,1}$ and $\lambda_{i,2}$. We used vague half-Normal hyper-priors (as per (Morales *et al.* 2004; Eckert *et al.* 2008)) on the parameters of the preceding priors.

Two thousand MCMC samples from the joint posterior distribution were obtained by running two chains each of length 20,000, discarding the first 10,000 samples as a burn-in and retaining every 10^{th} of the remaining samples (to reduce sample autocorrelation). We checked convergence of the model parameter and behavioural state estimates using the potential scale reduction factor (*R*-hat), calculated as the ratio between the pooled posterior variance estimate for all chains and the within-chain variance estimate (thus values close to 1 are consistent with convergence (Brooks & Gelman 1998)). The *R*-hat statistic was on average less than 1.07 for all parameter and behavioural state estimates.

Fur seal tracks are presented here as mean location estimates for the last 2000 model runs for each daily dawn and dusk period. Standard deviation values around these location estimates were 0.166 ± 0.056 and 0.210 ± 0.064 degrees of latitude and longitude respectively (n=32616 dawn/dusk location estimates). Given distances vary in relation to degrees with increasing latitude we have calculated distance of the last 500 model locations for each dawn and dusk period from the mean location for that period as 18.0 ± 0.6 km.

Chapter 3

South for the winter? Within-dive foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator

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Summary

1. Central to an animal's fitness is its foraging strategy and understanding the choices made by foraging animals is a fundamental aim in animal ecology. For diving animals, quantifying foraging effort within dives provides a measure of foraging that can be integrated with location information to reveal how animals use their environment as well as the trade-offs associated with contrasting foraging strategies.
2. We investigated the diving behaviour of 12 free-ranging Antarctic fur seals (*Arctocephalus gazella*) during their post-breeding winter migrations, quantifying within-dive foraging effort using a novel approach to identify divergent foraging strategies and determine the costs and benefits associated with foraging decisions.
3. Significant differences identified in both diving behaviour and foraging effort of female Antarctic fur seals could be attributed to two main, contrasting foraging strategies. Habitat was a major determinant of diving and foraging behaviour, with clear differences occurring either side of the Polar Front, a prominent oceanographic feature in the Southern Ocean.
4. Longer night duration and improved access to vertically migrating prey lead to increased foraging opportunities and a reduced foraging effort south of the Polar Front. Dives in this region were short and shallow. Conversely, seals remaining closer to the breeding colony north of the Polar Front had deep, long dives and an elevated foraging effort. The distinct foraging strategies of fur seals have associated trade-offs related to habitat availability, travel costs, prey accessibility and prey quality, which are likely driving their foraging decisions.

5. This study highlights the trade-offs between contrasting foraging strategies that currently co-exist within a population of a wide-ranging predator and raises questions about the viability of foraging strategies with future change to population size or environmental conditions. Finally, understanding the trade-offs associated with foraging strategies is important for assessing the foraging decisions of animals across a variety of environments.

Introduction

A fundamental aim in ecology is understanding the means by which animals acquire food. This is a problem that is faced by all animals, and a diverse array of strategies has evolved to facilitate food acquisition. A behavioural strategy, although an abstract concept, helps biologists consider how an animal's suite of behaviours affect its fitness (Breed *et al.* 2011). Central to an animal's fitness is its foraging strategy (Stephens & Krebs 1986), which incorporates the individual's energy requirements and the nature of the environment which they inhabit (McNamara & Houston 1986) in an often-complex manner. The interpretation of foraging strategies is dependent on the time-scale considered; short-term strategies (e.g. seasonal) may be nested in a broader principal strategy (e.g. annual, within a lifetime) (McNamara & Houston 2008). Theoretical frameworks such as Optimal Foraging Theory (MacArthur & Pianka 1966) are often used to evaluate the foraging strategies of animals, predicting that individuals should maximise energy intake while minimising the energy expenditure associated with prey searching, capture and handling. Air-breathing diving animals, typically mammals, birds and reptiles, are a unique case when examining foraging decisions because they forage in a three-dimensional environment, having to obtain prey that is dispersed throughout horizontal and vertical space (Kooyman 1989). Furthermore, the limitation of oxygen availability to the surface affects the foraging choices made by these animals (Mori 1998a).

With the advancement of bio-logging technology, considerable research has taken place into the horizontal, or two-dimensional, movements of marine animals at sea (Evans *et al.* 2013). Numerous studies characterised the migration pathways, foraging habitats and high-use areas of various marine species (e.g. Block *et al.* 2011). The collection of vertical movement data (i.e. depth) by tags also facilitates the investigation of dive behaviour and offers insights into how animals use the water column. The integration of diving parameters (dive duration, depth, surface interval etc.) with tracking data can provide a measure of an animal's habitat use in three dimensions. Furthermore, the development of indices to infer foraging behaviour (using track data, dive data or both) that is otherwise challenging or impossible to observe directly, can be used to examine foraging effort and patch quality (Womble *et al.* 2013), which are important aspects of an individual's foraging decisions.

For marine predators, diving behaviour varies markedly both between individuals of the same species (e.g. Ropert-Coudert *et al.* 2003) and within individuals (e.g. Guillemette *et al.* 2004; Sommerfeld *et al.* 2015), through a range of mechanisms. These mechanisms include experience, target prey type, capture techniques, morphological differences and habitat selection. For example, the diving behaviour of several species of pinnipeds including northern fur seals, *Callorhinus ursinus* (Nordstrom *et al.* 2013), southern elephant seals, *Mirounga leonina* (Hindell *et al.* 1991; James *et al.* 2012) and Antarctic fur seals, *Arctocephalus gazella* (Staniland *et al.* 2004; Lea *et al.* 2008; Goldsworthy *et al.* 2010), varies with region and foraging habitat. Differences in prey, metabolic requirements and foraging experience can also alter the diving behaviour of marine predators including penguins (Miller & Trivelpiece 2008; Scheffer *et al.* 2012), cetaceans (Baird *et al.* 2005), turtles (Sale *et al.* 2006) and pinnipeds (Lea *et al.* 2002b). The diving behaviour of marine animals is a central part of their foraging strategy. However, for many marine predators it remains unclear whether dive behaviour can be indicative of a broader foraging strategy and how diving behaviour is affected by the different foraging strategies employed.

Antarctic fur seals (AFS), one of the most numerous predators in the Southern Ocean, are an ideal model species to investigate the links between foraging strategy and diving behaviour. During the austral winter, female AFS are free from the constraints of reproduction and can undertake wide-ranging foraging migrations (Boyd *et al.* 2002; Staniland *et al.* 2012) encompassing a diverse range of habitats and potential prey types. Female AFS exhibit an assortment of winter foraging habitats throughout their circumpolar range (Mary-Anne Lea, unpublished data). Differences in foraging behaviour are also evident within populations, with animals from the same breeding location often utilising distinct foraging areas. In particular, AFS from Marion Island in the Southern Indian Ocean show high inter-individual variability in the number of winter foraging excursions undertaken, with some animals conducting a single, long distance trip of ~8 months duration, while others display central place foraging behaviour (Orians & Pearson 1979), undertaking multiple trips returning to the island to haul out (Arthur *et al.* 2015). Animals from this population occupy a variety of oceanic habitats during these trips, from south of the Antarctic Circumpolar Current to the northern extent of the sub-Antarctic Front, with approximately 40% of foraging occurring at or south of the Polar Front and 47% in sub-Antarctic Frontal waters more local to Marion Island (Mary-Anne Lea, unpublished data). In addition, stable isotope analysis of tracked animals reveals that winter diet varies with habitat and time of year, with seals feeding on mesopelagic fish and squid in sub-Antarctic and Polar Front waters and low trophic level prey including Antarctic krill (*Euphausia superba*) in southern waters (Walters 2014).

Evidently, Female AFS from Marion Island display a variety of winter foraging behaviours that differ in spatial, temporal and dietary aspects. The differential habitat use by seals will presumably have associated costs and benefits and the foraging decisions of individuals should reflect these. The trade-off in energy expenditure associated with travelling to remote southern foraging areas, for instance, is presumed related to prey type and availability (see Marginal Value Theorem, Charnov 1976). Concurrently, greater competition with other predators nearer to the colony and the depletion of local prey (known as Ashmole's Halo, Ashmole 1963) is also a consideration. Despite being one of the best-studied Southern Ocean consumers, the diving and foraging behaviour of AFS in the winter is virtually undocumented. Here, we examine the post-breeding diving ecology of AFS. By employing a novel metric to infer foraging effort from vertical movement data in Otariid seals, we aim to: (1) identify divergent foraging strategies and (2) determine the energetic trade-offs associated with the foraging decisions of a wide-ranging species.

Materials and methods

ANIMAL HANDLING AND INSTRUMENTATION

The study took place at Marion Island (46°54’S, 37°44’E), Prince Edward Islands, Southern Indian Ocean in 2012 and 2013. Breeding adult female AFS were captured between February and April towards the end of lactation when they disperse from breeding harems prior to commencing their winter migration. Females who had bred that season and who were therefore likely to return to the colony the following season, were selected. Animals were physically restrained and instrumented with a global location-sensing logger (GLS; Mk19, British Antarctic Survey, Cambridge, 16 x 14 x 6 mm, 2.5 g, 3 years light memory) to estimate at sea locations for the duration of the winter migration, and a Time Depth Recorder (TDR; Mk9-187-02, Wildlife Computers, Redmond, WA, 87 x 18 x 18 mm, 38 g, 64 MB) to record dive information. The GLS loggers were attached to a plastic flipper tag (Superflexitag®, Dalton Supplies, Henley-on-Thames, UK) inserted into the trailing edge of the fore-flipper (Staniland *et al.* 2012). Logger architecture, attachment techniques and calibration methods are detailed in Arthur *et al.* (2015). The TDRs were attached dorsally to the fur approximately 10 cm anterior to the rump using a two-part epoxy (Araldite K268, Ciba-Geigy Corp., Basel) (Lea *et al.* 2008). TDRs were programmed to record depth (± 0.5 m) every 1 s and light level every 2 s. Seals were recaptured and instruments recovered at the start of the following breeding season in November-December when pregnant females return to the colony to pup.

ANIMAL MOVEMENT METRICS

Location estimates for seals during their winter migrations were produced from the raw light and temperature data collected by the GLS loggers following the Bayesian approach of Sumner et al. (2009) using the R software (R Core Team 2014) package 'tripEstimation' (Sumner & Wotherspoon 2010). In summary, the posterior means for each twilight period were summarised from the accepted Markov Chain Monte Carlo samples, giving two location estimates per day (dawn and dusk). State-space models specific to geo-location data were then used to infer horizontal area-restricted search (hARS) behaviour, indicative of probable large-scale foraging (Patterson *et al.* 2008). Model design and implementation followed the framework of Jonsen *et al.* (2005). Full details of geo-location and state-space models are presented in Appendix S1 Supporting Information.

DIVING BEHAVIOUR ANALYSIS

Pre-processing

To account for drift in the pressure transducer accuracy affecting the zero depth reading, all depths were corrected using a customised Zero Offset Correction method (See Luque & Fried 2011). We considered a modal depth of between 10 and -5m as representative of the true surface across a moving two-hour window. This depth was then subtracted from all values in this interval to produce zero offset corrected depths. Only excursions to >6 m were analysed (Staniland & Robinson 2008) as we found the broken stick algorithm (below) typically did not fit dives shallower than this (see results).

Vertical area-restricted search activity

For each dive we calculated the maximum depth (m) and dive duration (sec). A dive residual was also estimated to determine whether the duration of dives for a given depth was longer or shorter than expected (e.g. Bestley *et al.* 2014). We used the Pearson residuals from a linear mixed effect model (LMM) fitted via restricted maximum-likelihood estimation (REML) with individual seal fit as a random term, using the R package 'nlme' (Pinheiro *et al.* 2014).

Traditionally, the dive profiles of air-breathing marine animals are viewed as having three distinct phases: descent, bottom and ascent. More recently, the miniaturisation and increased memory and battery life of bio-logging instruments has enabled the collection of dive data at very fine resolutions (i.e. less than 1s) (Evans *et al.* 2013) revealing that the dives of many marine animals are considerably more complex. It is likely that the three-phase view of dives leads to an over-simplification of dive behaviour and an under-estimate of foraging activity, particularly when relying on bottom phase alone to investigate foraging. As an alternative, we employed an automated vertical Area-Restricted Search (vARS) algorithm developed by Heerah *et al.* (2014), which identified the optimal number of segments that best explain a dive's profile. Initially, three points were used to define the dive profile (a surface start point, maximal depth and surface end point) after which we iteratively included the points of maximum difference between the original profile and the profile constructed by linear interpolation between points chosen during the previous iteration. An inflection point was identified, after which the amount of new information resulting from an increase in broken stick (BSt) points begins to decline. The number of BSt points (and hence segments) at the inflection point is then used to optimally summarize the dive profile (Heerah *et al.* 2014) (Appendix S2, Fig. S1). We found the BSt algorithm typically did not fit short and shallow dives, as the model could not detect an inflection point (see results). Consequently, only dives greater than 40 seconds duration were included in the analysis.

INFERENCE OF FORAGING ACTIVITY WITHIN DIVES

BSt segments were used to infer a behavioural mode based on the vertical velocity and sinuosity of their trajectory. For each segment between two BSt points we calculated the vertical rate of change (m/s) and the vertical sinuosity following the methods detailed in Heerah *et al.* (2014) adapted from Dragon *et al.* (2012). Vertical sinuosity is expressed as a ratio, with a value of 1 when the animal has maintained a straight path within a segment, decreasing towards 0 as the animal deviates to a more sinuous path. As was reported for southern elephant and Weddell seals, *Leptonychotes weddellii* (Heerah *et al.* 2014), we found the distribution of vertical sinuosity for AFS suggested two distinct behavioural modes (Appendix S2, Fig. S2). Based on this, we used a sinuosity threshold of 0.9 to distinguish between hunting (vertical area-restricted search – vARS; 0 - 0.9 sinuosity) and travelling (>0.9 sinuosity) modes for each BSt segment within a dive. We then calculated the total duration and proportion of each dive that was spent in vARS mode.

SPATIAL AND TEMPORAL RELATIONSHIPS WITH FORAGING EFFORT

Dive behaviour was integrated with location estimates to give an approximate location for each dive. The majority of dives, which occurred between two locations, were attributed to the nearest location in time. The inferred hARS state for each location was also appended to the dive record. For each location estimate, dive parameters were binned and averaged to obtain a mean value for each dive parameter. Dives were also binned by month. Based on location, each dive was assigned to one of 13 inter-frontal zones (IFZs). We used weekly frontal positions between 1992-2009 (Sokolov & Rintoul 2009a; 2009b) available from the Australian Antarctic Data Centre extracted using the R package 'raadtools' (Sumner 2015). Data were restricted to the winter months corresponding to seal locations and we calculated the average IFZ value for each cell across a 0.5 x 0.5 degree grid. This provided a long-term average position of fronts in the Southern Ocean for the winter period. These were then summarised into the eight major IFZs incorporating: 1. south of Antarctic Circumpolar Current Front - South (ACCF-S), 2. ACC to Polar Front – South (PF-S), 3. Polar Front (PF), 4. PF to sub-Antarctic Front (SAF), 5. SAF, 6. sub-Antarctic Front – North (SAF-N) to sub-Antarctic Zone (SAZ), 7. SAZ to sub-Tropical Zone – South (STZ-S), and 8. north of STZ-S.

Female AFS feed on vertically migrating prey and dive principally at night when prey are accessible closer to the surface (Boyd & Croxall 1992; Lea *et al.*

2002b). As a measure of foraging effort, we therefore calculated the total duration of vARS behaviour per night. Initially, the point at which each dive occurred in the diurnal cycle was estimated from solar elevation using the “crepuscule” function in the R package ‘maptools’ (Bivand & Lewin-Koh 2014) to split dives into separate night, day, dawn and dusk periods. For each night, all dives between dusk and dawn were assigned to the dusk location and the total diving and foraging duration was calculated for that location. The night length for each location was also estimated using the “crepuscule” function as a representative of the potential available foraging time at each location.

To quantify the effect of IFZ and month on the diving behaviour of AFS we fitted mixed effects models in the R package ‘lme4’ (Bates *et al.* 2014). Liner Mixed Models (LMMs) were fitted to assess the effects on dive residual and the proportion of the dive in vARS, while Generalised Linear Mixed Models (GLMMs) were fitted to a Gamma error structure and identity-link function for maximum dive depth, dive duration and cumulative dive hours due to the positive, continuous, right-skewed nature of these response variables. To determine the relationship between foraging effort, dive behaviour, IFZ and month, we fitted Gamma GLMMs with a log-link from the null model to the saturated model considering all possible combinations. Predictor terms were transformed to meet the assumptions of normality where necessary using log or arcsine transformation and were standardised via centring and scaling to facilitate model convergence and comparison of predictors. Models were ranked using Akaike’s Information Criterion (AIC) and the best model was determined using Akaike weights and delta AIC (Burnham & Anderson 2002). Seal identity was included as a random term in all models. All analysis was undertaken in R (R Core Team 2014) and t tests are two-tailed.

Results

Twelve adult female AFS from Marion Island were tracked in 2012-13. A total of 1914 location estimates and 86 766 dives were recorded during this period. Four individuals were sampled across both years, providing data for 16 seal-year combinations (Table 3.1). There was no clear consistent inter-year pattern for those animals tracked in both years, with only two seals (B051 and B200) displaying similar patterns across both years. Analyses were restricted to the period between mid-April and the end of August, effectively representing the post-breeding winter season, as only two TDRs logged data past August and a programming issue in 2013 caused most tags to cease sampling in June (Table 3.1). Individuals undertook between one and four foraging trips during this period (Table 3.1), including partial trips recorded when tags stopped functioning prior to trip completion. The BSt algorithm fitted 74 834 (86%) of the dives, failing to identify an inflection point for 11 932 (14%) dives which were typically short (<40 s) and shallow (<6m). Henceforth, all means are reported plus or minus standard deviation. On average, dive profiles were optimally described with 12.3 ± 1.4 segments. Among all seals the mean dive duration was 106.9 ± 43.3 s (range 42-515 s) and the mean maximum dive depth was 31.0 ± 20.1 m (range 6.5-196 m) (Table 3.1).

Table 3.1. Details of the 12 female Antarctic fur seals from Marion Island used in this study; including the years for which dive data were collected, seal mass at tag deployment and recovery, mass change, the number of winter foraging trips with dive data (including incomplete trips), the duration of time-depth recorder (TDR) records, the percentage of dives in three regions (N of PF = north of the Polar Front, PF = Polar Front, S of PF = south of the Polar Front) and average dive parameters for individuals. Means are presented ± standard deviation.

Seal ID	Year	Deploy Mass (kg)	Recover Mass (kg)	Mass Change (kg)	Trips	TDR record	Dives N of PF (%)	Dives at PF (%)	Dives S of PF (%)	Mean BSt[a] segments	Mean dive duration (s)	Mean max depth (m)	Mean duration vARS[b] (s)	Mean prop. vARS[b]
B041	2013	32	39	7	1	18/4 – 8/6	83	16	1	11.9 ± 1.3	130 ± 48	45.0 ± 23.9	57 ± 37	43 ± 20
B051	2012	41	35	-6	1	10/5 – 5/10	100	0	0	12.4 ± 1.4	112 ± 45	24.0 ± 12.5	62 ± 36	53 ± 18
	2013	34	39	5	1	18/4 – 9/6	100	0	0	12.1 ± 1.3	124 ± 46	40.0 ± 21.2	49 ± 31	39 ± 19
B116	2013	48	33	-15	1	20/4 – 8/6	2	39	59	12.5 ± 1.4	94 ± 38	26.3 ± 19.5	39 ± 27	40 ± 20
B120	2012	34	37	3	1	23/4 – 10/6	6	38	56	12.6 ± 1.4	90 ± 39	22.4 ± 18.3	40 ± 29	43 ± 19
	2013	36	37	1	2	30/3 – 11/8	87	3	10	12.4 ± 1.3	103 ± 40	34.1 ± 21.2	43 ± 27	42 ± 20
B133	2012	38	36	-2	1	23/4 – 21/6	5	6	89	12.6 ± 1.4	81 ± 31	19.1 ± 12.2	38 ± 24	46 ± 18
B149	2013	32	31	-1	1	21/4 – 6/6	100	0	0	12.2 ± 1.2	101 ± 30	36.2 ± 18.0	35 ± 23	34 ± 19
B161	2012	30	37	7	4	26/4 – 17/12	40	11	49	12.4 ± 1.4	106 ± 41	32.8 ± 18.8	46 ± 31	42 ± 20
	2013	38	34	-4	2	18/4 – 8/6	96	4	0	11.9 ± 1.3	128 ± 43	51.2 ± 23.2	48 ± 33	36 ± 19
B163	2013	36	29	-7	2	12/4 – 15/8	50	26	24	12.5 ± 1.3	87 ± 35	21.9 ± 14.5	39 ± 23	44 ± 19
B200	2012	35	50	15	1	22/4 – 30/5	79	21	0	12.9 ± 1.5	82 ± 29	23.2 ± 14.4	35 ± 22	41 ± 20
	2013	31	46	15	1	22/4 – 8/6	100	0	0	12.4 ± 1.4	112 ± 46	38.3 ± 25.6	44 ± 30	38 ± 19
B242	2013	27	29	2	1	19/4 – 9/6	29	70	1	11.9 ± 1.2	103 ± 34	35.2 ± 21.1	37 ± 21	37 ± 19
PP486	2013	24	31	7	2	14/4 – 8/6	85	5	10	12.1 ± 1.3	93 ± 31	29.8 ± 16.7	40 ± 23	42 ± 19
YR477	2013	37	32	-5	2	14/4 – 8/6	54	7	39	12.3 ± 1.4	95 ± 38	28.1 ± 19.4	44 ± 27	44 ± 19
										12.3 ± 1.4	107 ± 43	31.0 ± 20.1	49 ± 32	44 ± 20

[a]BSt, Broken Stick segments, [b]vARS, vertical Area-Restricted Search.

HORIZONTAL AND VERTICAL AREA-RESTRICTED SEARCH

The mean duration of the dive in vARS mode was 48.8 ± 32.2 s and the average proportion of dive in vARS mode was 44.2 ± 19.8% (Table 3.1). Dives that included vARS behaviour were, on average, shallower and longer than dives where no vARS behaviour was identified (Table 3.2). Of all location estimates, 827 (43%) were identified as likely hARS behaviour. Dives were distributed evenly across horizontal behavioural states, with 35 547 (48%) dives occurring in hARS areas and 39 287 (52%) dives associated with more direct travelling behaviour. Diving behaviour was distinctly different between the two horizontal behavioural states (Table 3.2), with dives at hARS locations on average shallower (GLMM, AIC=620 697, null AIC=623 065, see Table S1a) and longer (GLMM, AIC=757 482, null AIC=757 687, see Table S1b). A comparison of dive residuals showed that dives in hARS regions were significantly longer than expected for a given maximum depth compared with non-hARS dives (LMM, AIC=722 122, null AIC=722 584, see Table S1c). There was good agreement between ARS behaviour in the horizontal and vertical dimensions, with both the duration (LMM, AIC=352 273, null AIC=352 406, see Table S1d) and proportion (LMM, AIC=654 891, null AIC=656 127, see Table S1e) of the dive spent in hunting mode (vARS) greater for dives at hARS locations, indicating that inferring foraging behaviour through the identification of within-dive vARS states yields similar estimates to more conventional hARS methods.

Table 3.2. Comparison of mean ± SD dive parameters between vertical area-restricted search (vARS) and horizontal area-restricted search (hARS) dives for 12 female Antarctic fur seals from Marion Island, 2012-13. "In" refers to dives that were identified as area-restricted search behaviour while "Out" refers to dives during transit behaviour.

Dive Parameter	Vertical ARS		Horizontal ARS	
	In	Out	In	Out
Maximum depth (m)	30.9 ± 19.8	42.2 ± 24.4	27.7 ± 17.2	33.9 ± 21.9
Dive duration (s)	107.7 ± 43.3	81.1 ± 34.4	108.3 ± 43.9	105.7 ± 42.7
Dive residual	2.1 ± 29.8	-38.3 ± 22.7	1.7 ± 31.0	0.4 ± 29.7
Duration dive vARS (s)	-	-	54.3 ± 34.3	43.8 ± 29.3
Proportion dive vARS (%)	-	-	47.9 ± 19.3	40.8 ± 19.7

SPATIAL AND TEMPORAL EFFECTS ON DIVE BEHAVIOUR

Seals dived across a variety of oceanic habitats, with dives recorded in five IFZs ranging north of Marion Island to the SAF and south to the ACCF-S (Fig. 3.1). There was a spatial pattern in diving behaviour, with dive duration and maximum depth in particular varying with location (Fig. 3.2). A prominent change in dive behaviour was associated with the PF, with dives south of the PF noticeably shallower and shorter than dives further north (Table 3.3, Fig. 3.2). As several IFZs had relatively few observations, dives were pooled into three regions reflecting this change in behaviour for comparison: north of the PF (N of PF), the PF, and south of the PF (S of PF). There were inter-individual differences in the use of these regions (Fig. 3.3). Six seals performed >20% of their dives S of PF, with two individuals (B116 and B133) concentrating the majority of their dives in this region. One individual (B242) dived mostly at the PF, while the remaining animals dived mostly N of PF, with two individuals (B051 and B149) diving exclusively in this region. Half of all seals spread their dives across regions, performing more than a third of their dives outside their most utilised region (Table 3.1). The mean deployment mass of seals (Table 3.1) was not significantly different for those that performed >20% of their dives S of PF (37 ± 6 kg) compared with animals which dived at or N of PF (33 ± 5 kg; t_9 = -1.43, *P* = 0.19). Seals exploiting the S of PF region, on average, lost mass during foraging trips (-3 ± 7 kg) compared with N of P and PF foragers (4 ± 7 kg), however this was not statistically significant (t_9 = 1.87, *P* = 0.09).

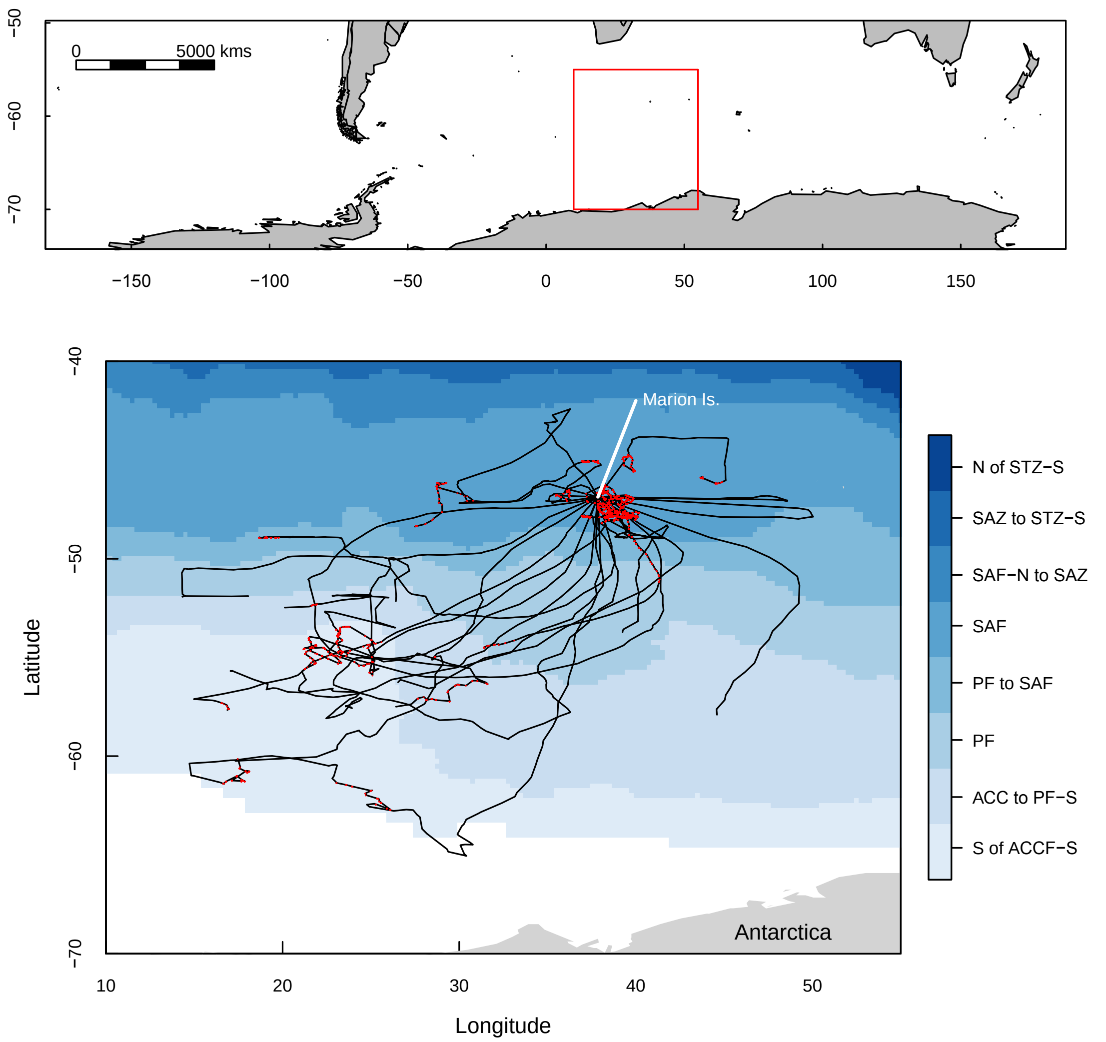

Figure 3.1. Winter migrations for 12 adult female Antarctic fur seals (*Arctocephalus gazella*) from Marion Island in 2012 and 2013. Tracks are coloured by behavioural state with lines and points representing transit and horizontal area-restricted search behaviour (hARS), respectively. Shading represents the average position of major inter-frontal zones (S of ACCF-S = south of Antarctic Circumpolar Current Front – South, ACC to PF-S = Antarctic Circumpolar Current to Polar Front – South, PF = Polar Front, PF to SAF = Polar Front to sub-Antarctic Front, SAF = sub-Antarctic Front, SAF-N to SAZ = sub-Antarctic Front – North to sub-Antarctic Zone, SAZ to STZ-S = sub-Antarctic Zone to sub-Tropical Zone – South, N of STZ-S = North of sub-Tropical Zone – South).

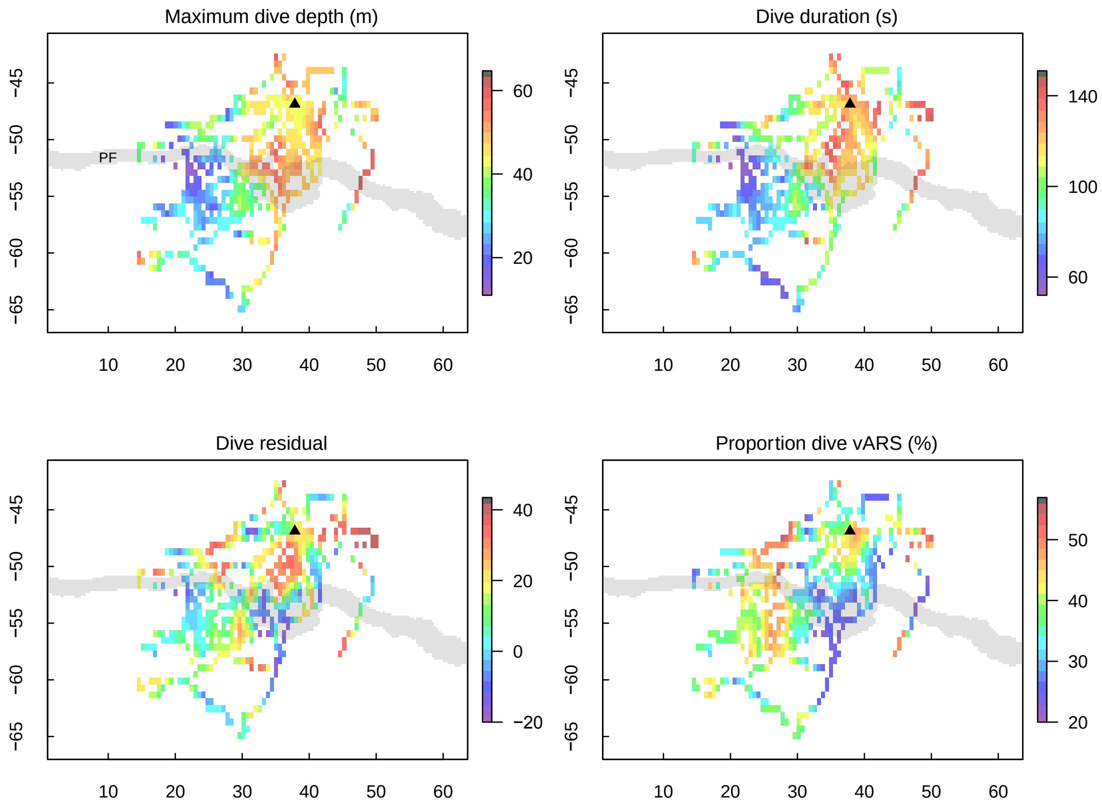

Figure 3.2. Gridded mean estimates of maximum dive depth (m), duration (s), dive residual and proportion of the dive in vertical area-restricted search (vARS) mode for Antarctic fur seals from Marion Island (black triangle). The shaded area represents the average position of the Polar Front (PF). Parameters were gridded and aggregated across all neighbouring cells, reducing the grid resolution by a factor of three and smoothing the data in a similar manner to k-nearest neighbour interpolation using cells rather than discrete points. The smoothed data was then resampled back across the original grid, excluding those cells with no observations.

Table 3.3. Mean ± SD dive parameters for the five summarized inter-frontal zones in which Antarctic fur seal dives were recorded. Mean parameter values for the three pooled habitat regions are presented in bold.

Inter-frontal Zone[a]	Max. depth (m)	Duration (s)	Dive residual	Duration Foraging (s)	Prop. dive vARS	hARS mode
Region N of PF	**33.1 ± 20.1**	**113.5 ± 43.3**	**1.4 ± 31.6**	**52.7 ± 33.1**	**0.45 ± 0.19**	**1.68 ± 0.38**
SAF	31.7 ± 18.9	112.9 ± 44.3	0.8 ± 31.9	53.5 ± 33.3	0.45 ± 0.19	1.74 ± 0.38
SAF to PF	40.8 ± 23.7	117.1 ± 44.0	5.0 ± 29.5	48.3 ± 31.2	0.40 ± 0.19	1.39 ± 0.27
Region PF	**34.9 ± 22.9**	**103.4 ± 41.1**	**-2.3 ± 26.2**	**38.1 ± 24.9**	**0.37 ± 0.20**	**1.11 ± 0.22**
Region S of PF	**20.6 ± 14.3**	**80.7 ± 27.2**	**-1.9 ± 18.1**	**35.9 ± 20.4**	**0.43 ± 0.18**	**1.49 ± 0.38**
PF-S to ACC	25.7 ± 18.6	87.7 ± 32.8	-2.6 ± 22.5	35.3 ± 21.8	0.40 ± 0.19	1.29 ± 0.34
S of ACC-S	18.5 ± 11.5	78.5 ± 25.8	-1.7 ± 15.9	36.2 ± 19.8	0.44 ± 0.17	1.57 ± 0.36

[a]SAF, sub-Antarctic Front; PF, Polar Front; ACC, Antarctic Circumpolar Current; Prop. dive vARS, proportion of the dive in vertical area-restricted search behaviour, hARS mode, horizontal area-restricted search value.

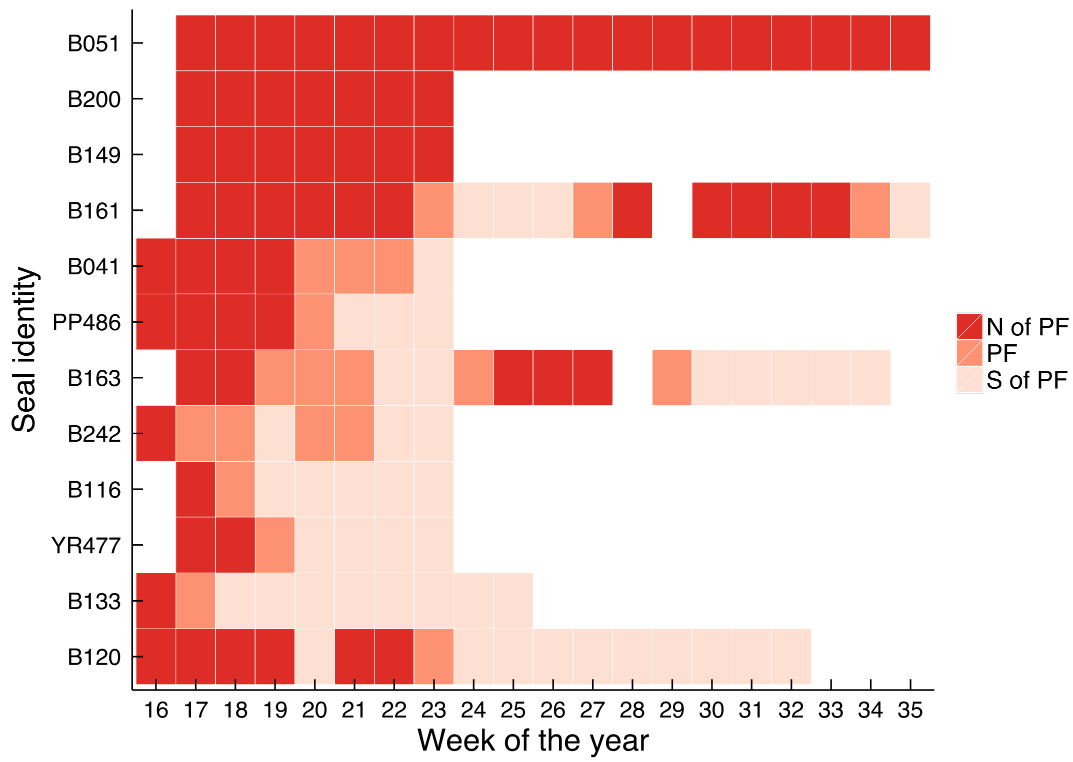

Figure 3.3. Heatmap of the weekly use of three habitat regions by 12 female Antarctic fur seals from Marion Island over the winter season from the start of April (week 16) to the end of August (week 35). N of PF = north of the Polar Front, PF = Polar Front, S of PF = south of the Polar Front. Note: seals B161 and B163 hauled out for the weeks 28 and 29 respectively.

Maximum dive depth varied by region and month (GLMM, AIC=607 881.9, null AIC=623 065.2). Dives S of PF were shallower than dives either at the PF or N of PF (Fig. 3.4, see Table S2a). The depth distribution of within-dive foraging segments reflected this pattern, with seals appearing to forage across a range of deeper depth when N of PF (Fig. 3.5a). On average, dives were deepest in April and became progressively shallower until July, when dives were shallowest. This pattern was evident across all three regions (Fig. 3.4). Dive duration also varied by region and month (GLMM, AIC=743 407.8, null AIC=757 687.5), with dives becoming shorter in more southerly regions (Fig. 3.4, see Table S2b). Surprisingly, dive duration displayed the opposite temporal trend to depth, with dives in the early post-breeding period shorter than dives in late winter (see Table S2b). The distribution of dive residuals across the season reflects this relationship (LMM, AIC=708 836.2, null AIC=722 584.2), with negative residuals in early winter (i.e. dives shorter than expected for a given depth), becoming positive from June (i.e. dives longer than expected for a given depth, Fig. 3.5b, see Table S2c). On average, dives N of PF had positive dive residuals, suggesting dives were longer than expected for their depth, whereas dives S of PF had negative residuals, indicating they were shorter than expected (see Table S2c). The average duration of dives in vARS mode varied with region and month (GLMM, AIC=718 316.9, null AIC=728 185.8, see Table S2d), as did the proportion of each dive in vARS mode (LMM, AIC=646 437.1, null AIC=656 127.2). Unexpectedly, dives N and S of PF had a much greater proportion of the dive in vARS mode than dives at the PF, where the proportion was relatively low (Fig. 3.2, see Table S2e). The mean duration of dives in vARS mode increased through the season, broadly following the temporal trend of dive residuals (Fig. 3.5c).

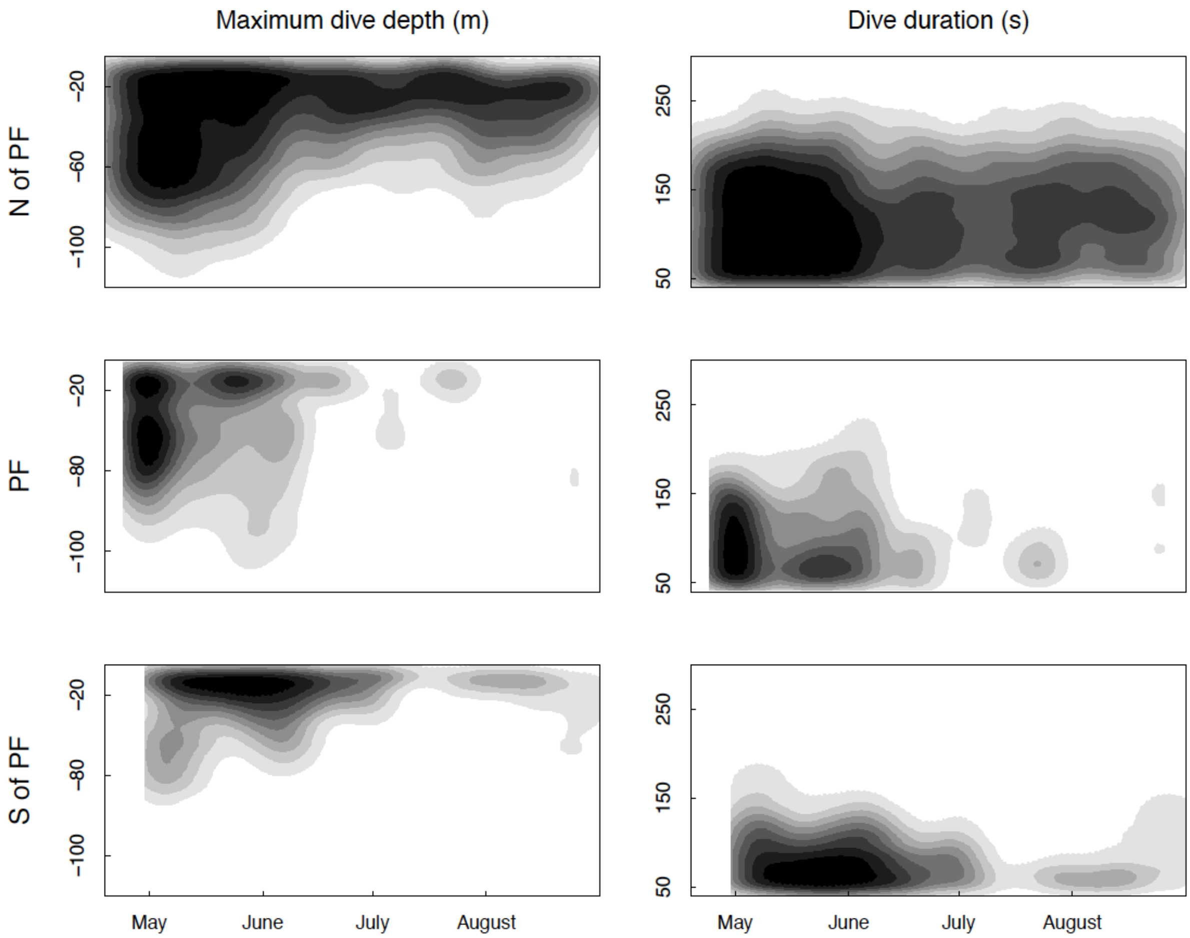

Figure 3.4. Kernel density plots of the spatial and temporal distribution of maximum dive depth (m) and dive duration (s) values. Darker colours indicate high density. For each variable, vertical panels are split into the three major habitat regions. N of PF = North of the Polar Front, PF = Polar Front, S of PF = South of the Polar Front.

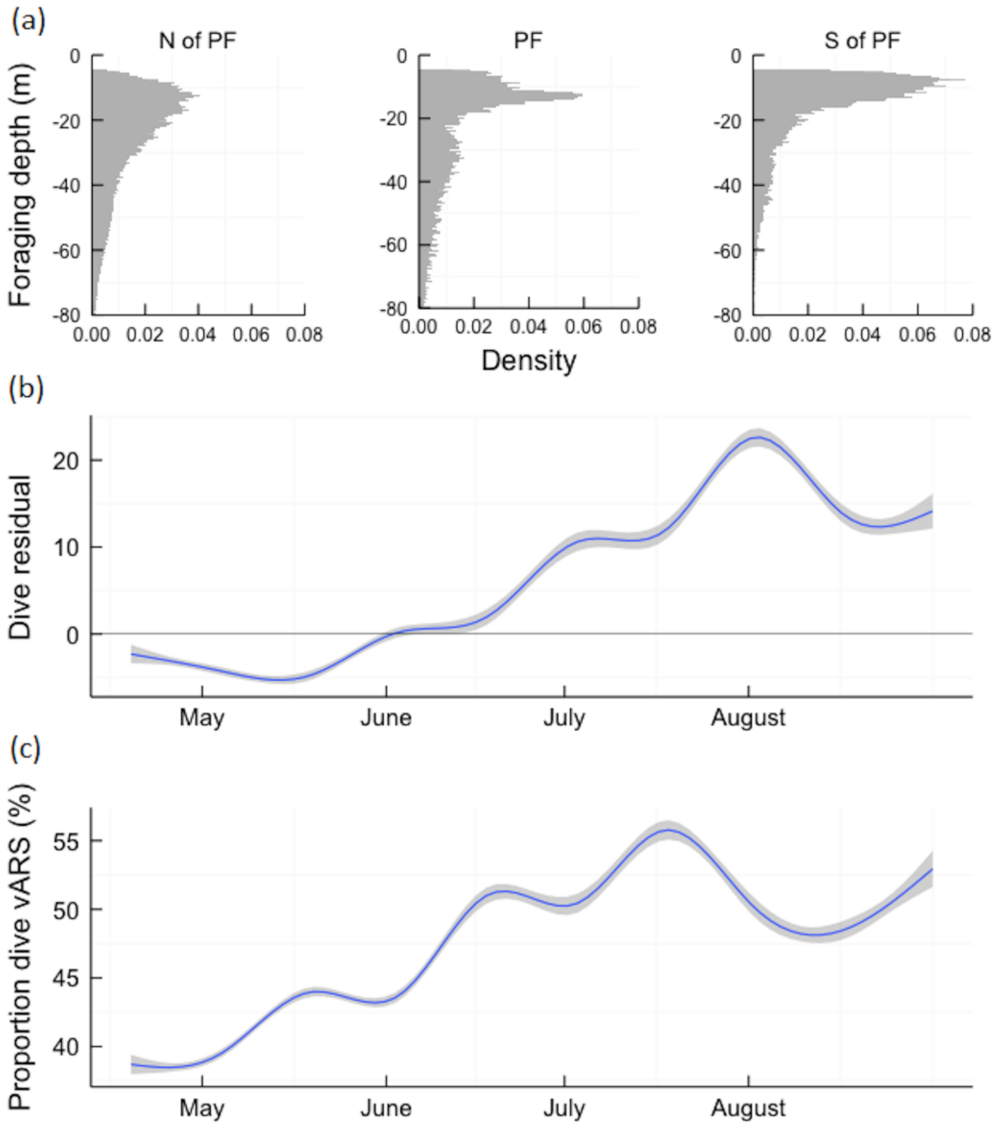

Figure 3.5. (a) The density distribution of foraging segment depths across the three regions is shown in the bottom panels. N of PF = North of the Polar Front, PF = Polar Front, S of PF = South of the Polar Front. **(b)** Distribution of dive residuals and **(c)** proportion of the dive in vertical area-restricted search (vARS) mode over the austral winter. Data were fitted to a loess smoother with the estimate and standard error shown by the line and shaded area, respectively. Dive residuals are from a linear mixed effect model of dive duration and maximum depth with seal identity fitted as a random term.

SPATIAL AND TEMPORAL EFFECTS ON FORAGING EFFORT

The potential available foraging time for seals, represented by night length, was dependent on latitude and time of year. At 40°00’S (near the northern range of tracked animals, Fig. 3.1) in early and late winter, approximately 13 hours of potential foraging time were available to seals, compared with over 20 hours at 65°00'S in mid-winter (Fig. 3.6). In June and July, approximately six more potential foraging hours were available to animals at 65°00'S than for animals foraging north of Marion Island, although the latitudinal differences were less pronounced closer to the equinoxes in early and late winter (Fig. 3.6).

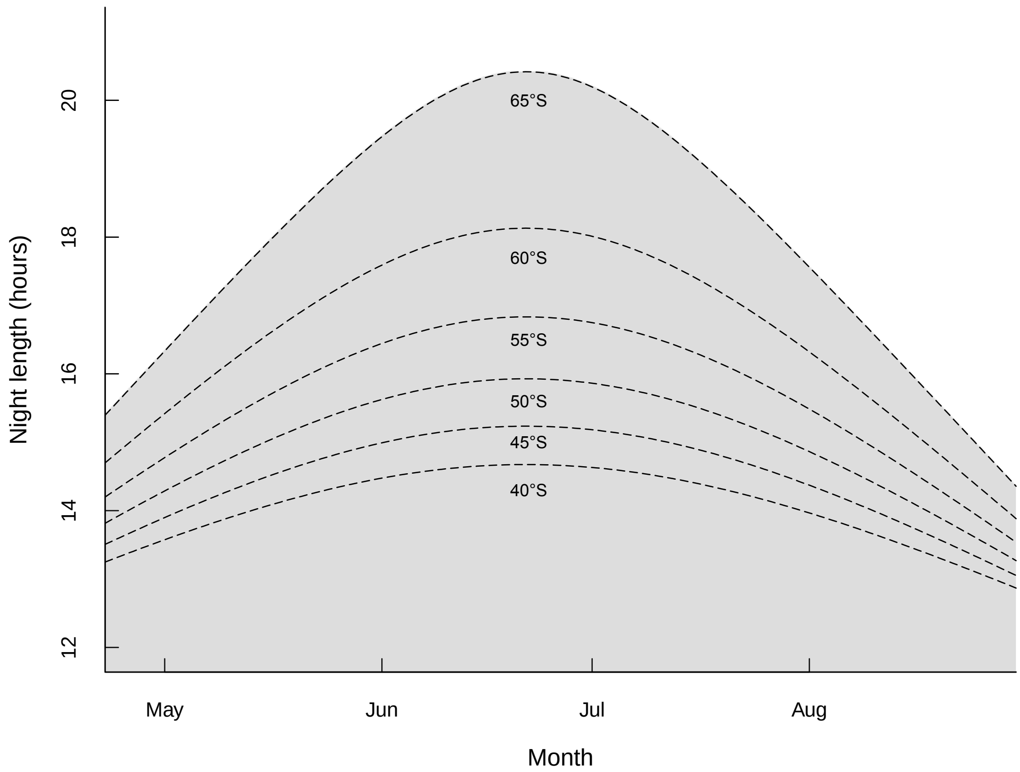

Figure 3.6. Winter night duration for six locations at five-degree intervals along a latitudinal gradient (located at 37°00'E, transecting Marion Island) spanning the approximate latitudinal range of 12 female Antarctic fur seals from Marion Island. The shaded area represents the hours of darkness.

Diving effort, measured as cumulative dive hours per night, had a negative relationship with night length. On average, diving effort was greatest N of PF, declining with latitude to be least S of PF, where nights are longer and potential foraging hours are greatest (Fig. 3.7, GLMM, AIC=2900.5, null AIC=3088.5, Table

S2f). Diving effort also varied by time of year, although this relationship was dependent on region (Fig. 3.7). The spatial and temporal patterns observed in the diving behaviour of female AFS over post-breeding winter were reflected in their inferred foraging effort (time in vARS). We compared the effect of region, month, maximum depth, dive residual, proportion of dive in vARS and night length on the total hours of foraging behaviour per night. The best model was the full model including all predictor terms (AIC weight = 0.720; Table 3.4). Based on this model we found that foraging hours per night were greatest N of PF and decreased with latitude. On average, foraging hours were greatest in April, decreasing in subsequent months (Table S2g), however this relationship varied with region (Fig. 3.7). Foraging hours were highest when nights were shorter, average dive depths were deeper and the average proportion of dive in vARS was greater (Table S2g).

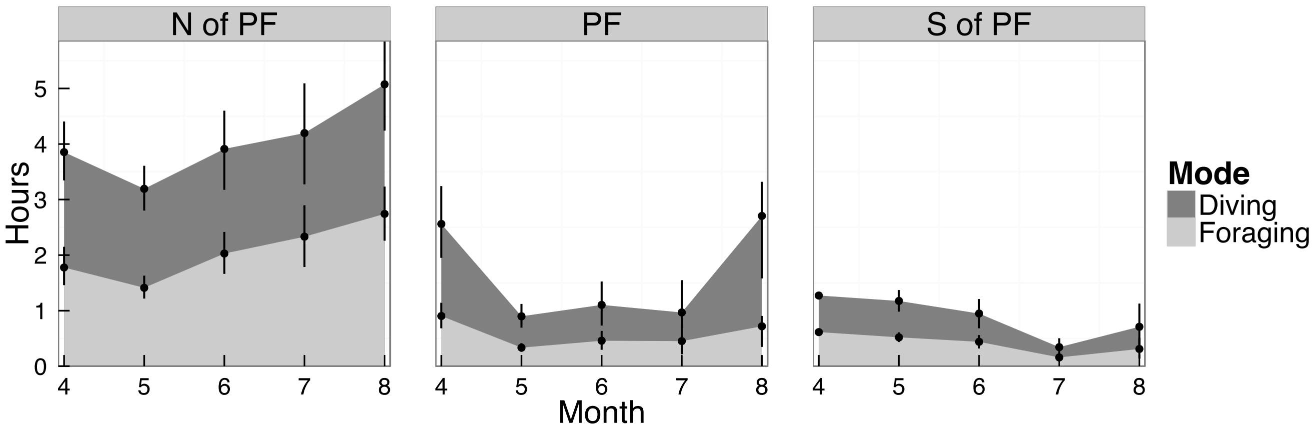

Figure 3.7. Nightly diving (dark grey) and foraging (light grey) hours averaged by month and region for 12 female Antarctic fur seals from Marion Island 2012-13. Black bars represent the 95% confidence interval. N or PF = North of Polar Front, PF = Polar Front, S of PF = South of Polar Front.

Table 3.4. Summary of generalised linear mixed-effect models (GLMMs) examining the relationship between foraging time, dive behaviour, region and month (forage hours = foraging hours per night, prop. dive vARS = proportion of the dive in vertical area-restricted search behaviour). Only models with a delta AIC <10 are shown and the accepted model is presented in bold.

Candidate models	*k*	LL	AIC	ΔAIC	*w*AIC
1. foraging hrs ~ dive resid. + max. depth + month + night length + prop. dive vARS + region	**8**	**-472.9**	**972.4**	**0.0**	**0.720**
2. foraging hrs ~ dive resid. + max. depth + month + prop. dive vARS + region	7	-475.0	974.4	2.0	0.261
3. foraging hrs ~ dive resid. + max. depth + month + night length + prop. dive vARS	7	-478.7	979.6	7.3	0.019

k, number of parameters; LL, log-likelihood; AIC, Akaike's Information Criterion; **Δ**AIC, difference in AIC from that of the best fitting model; *w*AIC, AIC weight.

Discussion

DIVING MODELS AND INFERENCE OF FORAGING

The broken stick (BSt) method used to describe dive profiles and infer foraging in marine predators is a relatively new approach that has not been directly validated on this species. The BSt algorithm failed to fit a higher percentage of AFS dives (14% not fitted) than Southern elephant seal (6%) or Weddell seal (4%) dives (Heerah *et al.* 2014), probably because AFS perform more short and shallow dives compared with these species. Despite this, fur seal dives were optimally described by an almost identical number of segments per dive (12.3 for AFS compared with 12 for elephant seals and Weddell seals). Two distinct behavioural modes were identified based on the vertical sinuosity of BSt segments similar to Heerah et al. (2014), giving us confidence that the approach is suitable for analysing the dives of this species. Vertical sinuosity is indicative of prey searching in Southern elephant seals (Gallon *et al.* 2013) and short periods of elevated changes in depth during the descent phase of AFS dives correlate with increased prey-capture attempts (Viviant *et al.* 2014), suggesting that the inference of foraging behaviour based on the vertical sinuosity of dive segments is appropriate for AFS.

We found general agreement between the two methods of inferring foraging effort, with ARS behaviour deduced from horizontal tracking data (hARS) a good indicator of within dive ARS behaviour (vARS). This is similar to the findings of Dragon *et al.* (2012) who showed that active foraging dives in Southern elephant seals were more numerous when animals were displaying horizontal area-restricted search behaviour. Ramasco *et al.* (2015) also observed that movement responses that lead to an intensification of ARS behaviour in harbour seals (*Phoca vitulina*) were positively related across horizontal and vertical dimensions. When female AFS dived in areas of hARS behaviour, dives were typically shallower and longer, with positive dive residuals. This differs from Bestley *et al.* (2014) who found the probability of AFS switching into a resident hARS state during summer foraging to be positively associated with shallower but shorter dives. However, the five seals in that study were all male, which are larger and exhibit markedly different dive behaviour to females (Staniland & Robinson 2008).

CONTRASTING FORAGING STRATEGIES

When explaining how marine predators adapt their diving behaviour to different foraging environments there are two competing hypotheses. The first centres on the animal's physiology in relation to oxygen depletion and reacquisition, suggesting that an increased travel time to foraging depth should be compensated for by energy gain (Kramer 1988). Longer dive durations generally indicate increased foraging success under this scenario (e.g. Austin *et al.* 2006). An alternative hypothesis builds on this to include considerations such as prey quality and distribution (e.g. Mori 1998a). In this instance, a greater time at foraging depth does not necessarily increase foraging success. In particular, animals foraging in high quality patches are assumed to have high prey capture rates and should, therefore, spend less time there (Charnov 1976). Empirical findings from a range of species do not consistently support either hypothesis (Bestley *et al.* 2014). However, in poor quality patches, female Antarctic fur seals increase their foraging effort by diving more and spending more time searching for prey at the bottom of dives (Mori & Boyd 2004; Viviant *et al.* 2014). In light of this, and considering the ecological nature of our study, we interpret positive dive residuals to indicate that dives were longer than expected for a given depth because of increased searching times, while negative residuals indicate dives that were shorter than expected because prey were encountered early in the dive. The positive dive residuals, longer dive duration and increased proportion of vARS behaviour observed for animals foraging N of PF in our study are in line with this.

Based on dive behaviour and foraging effort, AFS from Marion Island exhibited two major strategies during their post-breeding winter foraging migrations. Seals displayed a greater proportion of both vARS and hARS behaviour N of PF and S of PF, with reduced ARS behaviour in the PF region, a surprising result given the usage of this profitable region by several apex predator species (Bost *et al.* 2009). It appears that animals will stay N of PF, remaining in SAF waters typically in close proximity to Marion Island to forage, or transit S of PF to forage. Half of all animals undertook greater than 80% of their dives in a single region, indicating this choice of strategy is potentially strong. However, the remaining half dived approximately evenly across more than one region, suggesting a combination of these two major strategies is often employed rather than a discrete choice between the two. Our findings support those of a breeding season study by Staniland *et al.* (2004), which concluded that location is a primary determinant of diving and foraging behaviour in AFS. Differences in the diving and foraging behaviour of marine predators between Southern Ocean frontal zones, similar to those reported here, are known for several species (Bost *et al.* 2009) including Southern elephant seals (Biuw *et al.* 2007) and king penguins *Aptenodytes patagonicus* (Scheffer *et al.* 2012) and can be linked to differences in prey type and availability.

The foraging decisions of wide-ranging animals should operate to maximise energy intake while minimising energy expenditure (MacArthur & Pianka 1966), with different foraging strategies likely to have differing associated costs and benefits. For female AFS, there is a clear benefit in travelling S of PF during trips to sea as night length increases with latitude during the austral winter. As AFS typically target vertically migrating prey that are accessible at night (Boyd & Croxall 1992; Biuw *et al.* 2009), any differences in night length represent inequalities in available foraging time and access to prey, favouring those animals foraging further south. Differences are most pronounced in mid-winter, when the available foraging time at southern habitats is up to six hours greater than northern habitats close to Marion Island. However, there are energetic costs associated with foraging S of PF including increased travel costs (see Marginal Value Theorem, Charnov 1976) and the additional thermoregulatory requirements that accompany high latitude waters in winter. Such costs are likely to be less for animals remaining N of PF. We did not, however, find any significant differences in size between seals favouring either strategy. However, weighing of animals upon return to the colony was opportunistic on the first sighting, meaning that some individuals were weighed before pupping and others after, potentially biasing these results.

Despite enhanced foraging opportunities S of PF, seals in this region had a reduced dive effort, diving for approximately a third as many hours per night, than animals that remained N of PF (1.0 ± 1.2 vs 3.8 ± 3.6 hours). The diving intensity of marine predators is often linked to prey availability and patch quality (Monaghan *et al.* 1994; Mori 1998b). For AFS at Kerguelen Island, also in the Southern Indian Ocean, increased dive effort was correlated with reduced foraging success and/or low quality patches (Viviant *et al.* 2014). Although we have no direct measure of foraging success here, foraging effort differed by region, indicating that animals N of PF were foraging for significantly longer per night than those foraging S of PF, suggesting that average foraging success is higher in southern habitats and seals become satiated faster.

We observed regional variation in the diving behaviour of AFS during their winter migrations. Dives S of PF were relatively shallow and shorter than predicted based on negative dive depth residuals, compared with dives N of PF which were deeper and longer with positive dive residuals. The diving behaviour of air-breathing animals is often used to explain and predict the use of prey resources and numerous theoretical models exist on this topic. Thompson and Fedak (2001) assessed dive duration considering patch quality and oxygen balance and predicted that for shallow dives, there is a benefit in terminating dives when no prey are encountered early in the dive. However, for deeper dives, the benefit of terminating is reduced. The regional differences in dive depth and duration observed in this study seemingly conform to this model. The dives of seals S of PF were shallow and shorter than expected, with seals presumably benefiting from terminating if no prey were encountered early in the dive. Conversely, dives N of PF were deep and longer than expected, presumably with a reduced benefit to animals in terminating their dives if prey isn't encountered early. Thompson and Fedak (2001) relate this to patch quality. However, we suggest the differences observed for AFS can be related to different target prey, rather than the overall quality of foraging patches. Disregarding any potential costs of transiting to S of PF, our results indicate that AFS foraging N of PF are "working harder" than those foraging further south.

A recent study by Walters (2014) revealed that the winter diet of female AFS from Marion Island varies spatially, with animals largely feeding on mesopelagic fish and squid at or N of PF, while lower trophic level zooplankton, principally Antarctic krill (*Euphausia superba*), were important dietary components for animals foraging in more southerly inter-frontal zones. Pairing these findings with ours suggest that animals travelling S of PF during winter are targeting lower trophic level prey, including krill, that are more numerous and/or predictable further south in the Southern Indian Ocean closer to the pack-ice zone (Nicol *et al.* 2000a; Siegel 2005) leading to reduced dive and foraging effort. Concomitantly, seals N of PF are likely feeding on mesopelagic fish that are energy rich (Raclot *et al.* 1998; Lea *et al.* 2002a; Tierney *et al.* 2002), widely dispersed (Sabourenkov 1991) and relatively deeply distributed in the water column at night (Collins *et al.* 2012), compelling animals to intensify their diving and foraging effort. We suggest that the differences in dive and foraging effort reported here are driven primarily by differences in target prey. Walters (2014) also reports temporal variation in the winter diet of AFS, with seals shifting to a diet of dominated by energy-rich mesopelagic fish and squid during the pre-breeding period. Although our study does not extend into spring, we note a general trend of increasing diving and foraging effort towards the end of winter (July to August) with more positive dive residuals (dives longer than expected), which suggests a shift towards higher trophic prey based on the spatial patterns observed in this study. The trend coincides with increasing ocean productivity in the Southern Ocean during spring (e.g. Smith & Nelson 1990; Bathmann *et al.* 1997) as well as the increasing energetic demands of gestation after delayed implantation in autumn typical of otariid seals (Bester 1995; Boyd 1996).

At South Georgia, in the Southern Atlantic Ocean, AFS feed mainly on Antarctic krill and fish (Boyd *et al.* 1991; Reid & Arnould 1996). South Georgia is the primary breeding population of this species, having undergone rapid growth since the 1930's to number over 4 million animals representing over 95% of today's global population (see Staniland *et al.* 2011). Such sustained, rapid population growth implies that krill is a valuable prey resource. Indeed, annual variations in the local availability of krill at South Georgia are a limiting factor that can affect the reproductive success of top predators in the ecosystem (Croxall *et al.* 1999). The distribution of krill throughout the Southern Ocean is heterogeneous, with the Scotia Sea and areas around South Georgia supporting a greater long-term density of krill than the waters south of Marion Island (see Atkinson *et al.* 2004). With recent work revealing krill as an important prey item for a proportion of the Marion Island fur seal population (Walters 2014), it is plausible that the co-occurrence of two contrasting foraging strategies in this population is connected to the potentially limiting distribution of krill prey in this region.

For contrasting foraging strategies to persist in a population, it follows that neither strategy will offer a significant benefit in net energy gain over the long term compared with the other. We found no significant difference in mass change between strategies, despite a suggestion that seals foraging N of PF gained more mass than those foraging S of PF. Future data from more individuals would help clarify this relationship. Potentially, the two main foraging strategies of female AFS from Marion Island are equally favourable and may even be considered evolutionarily stable strategies (ESS, Smith & Price 1973) that cannot be outcompeted or replaced by alternate strategies. However, the foraging strategies of AFS are unlikely to be heritable (a condition of ESS's), instead being developed on an individual basis with age and experience, and it is doubtful that either strategy is entirely robust to challenge. Despite the southern strategy being less common, with fewer animals diving chiefly S of PF, we suggest it persists in the population as the energetic trade-offs are not high enough to discourage it. Furthermore, AFS recolonised Marion Island circa 50 years ago (see Hofmeyr *et al.* 1997) and the population has since grown rapidly, with an annual rate of increase as high as 17% (Hofmeyr *et al.* 2006) and a current annual production of approximately 1500 pups (Wege *et al.* 2016) Although population growth has slowed in recent years (Wege *et al.* 2016), continued population growth may impact the viability of either strategy through factors such as increased intra-specific competition. Future projected climate scenarios for the Southern Ocean also raise questions about the longevity of these strategies. With predicted changes to winter sea ice coverage and the warming of surface waters likely to cause the pole-ward shift of major frontal zones (IPCC 2007; Mayewski *et al.* 2009), changes to the profitable foraging regions of top predators are likely to result (e.g. King penguins; Péron *et al.* 2012). It is conceivable that the S of PF strategy exhibited by female AFS from Marion Island will become energetically more costly because of increased travel distances, favouring remaining N of PF to forage despite the elevated foraging effort that accompanies this strategy. Concurrently, continued warming of the already warmer waters N of PF may impact the distribution of prey resources, through a range of mechanisms including a southward shift in range or retreating to deeper depths to avoid warmer waters (Flores *et al.* 2012), and ultimately affect the foraging success in waters local to the breeding colony. Future investigation of energetic and demographic responses is key to understanding the long-term viability and co-existence of disparate foraging strategies in wide-ranging species such as fur seals.

Conclusion

Using a within-dive foraging metric, we show that the diving behaviour of a wide-ranging marine predator can reveal its broader foraging strategy. The diving behaviour of female AFS was strongly influenced by their choice of foraging region, a central component of foraging strategy. Differences in dive behaviour and foraging effort reflected divergent foraging strategies, with two distinct winter strategies identified for female AFS from Marion Island. These foraging strategies have associated energetic trade-offs that animals consider when making judicious foraging choices and are key to understanding the decisions of foraging animals and the mechanisms that facilitate the co-existence and viability of divergent strategies. Future work understanding how animals settle on particular foraging strategies (i.e. juvenile dispersal, social facilitation and experience) and the factors affecting the long-term persistence of these strategies, is important for assessing the broader implications of foraging decisions on a life-time scale.

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Supporting Information

Appendix S1. Methods section of Lea *et al.* (unpublished data) detailing the location estimation and state-space modelling procedures employed (Presented in Supporting Information Chapter 2).

Appendix S2. Graphical representations of the broken stick approach.

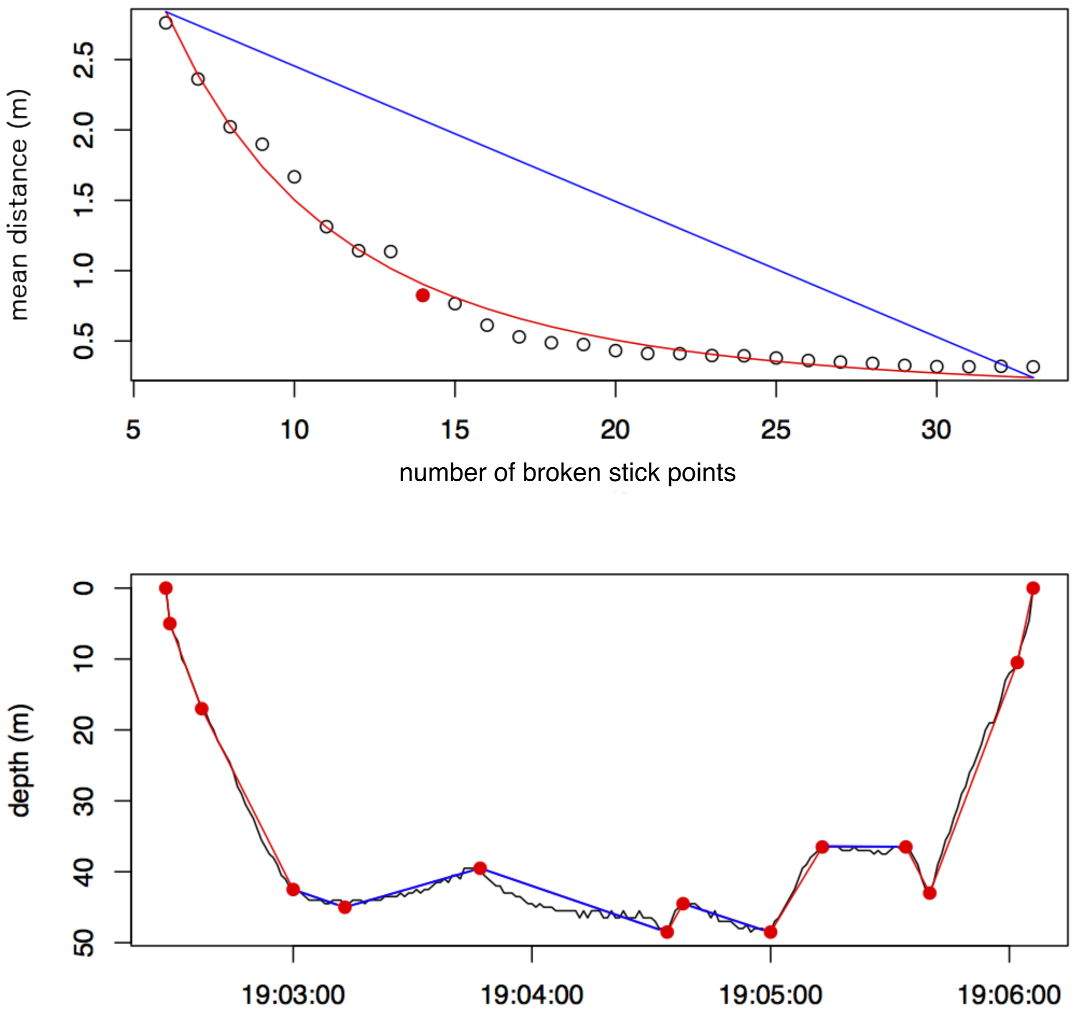

Figure S1. **Example of the broken stick analysis for one dive.** The inflection point (shown in red on the top panel) is the point at which the amount of new information resulting from an increase in points begins to decline. The resultant segments that optimally summarise the dive profile are shown in the bottom panel, where red lines represent travelling segments and blue lines represent hunting (vARS) segments.

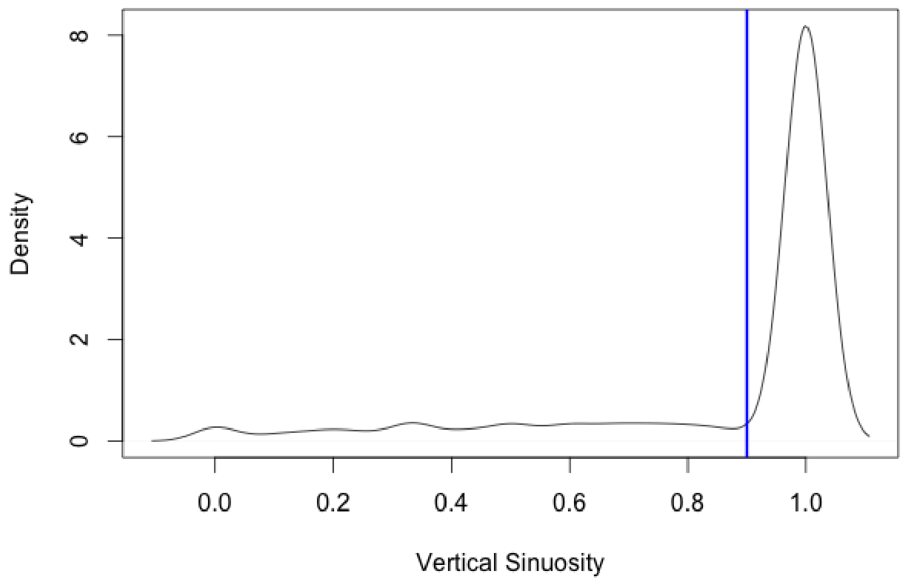

Figure S2. The distribution of sinuosity values. The sinuosity threshold of 0.9 is represented by the blue line.

Appendix S3. Results of mixed models.

Table S1. Results of mixed models examining the effects of hARS mode on the dive behaviour and foraging effort of female Antarctic fur seals. Generalised Linear Mixed Models (GLMMs) were fitted to maximum dive depth and dive duration while Linear Mixed Models (LMM) were fitted to dive residual, proportion dive vARS and log-transformed duration dive vARS. Seal ID was fitted as a random term in all models.

Parameter[a]	Variance	Estimate	SE	95% CI
(a) *Maximum dive depth*				
Fixed – Intercept		0.039	0.003	0.034, 0.045
non-hARS		0.008	0.001	0.007, 0.009
Random – Seal ID	3.07e-05			
(b) *Dive duration*				
Fixed – Intercept		1.04e-02	3.82e-03	9.66e-03, 1.11e-02
non-hARS		-4.83e-04	3.33e-05	-5.48e-04, -4.17e-04
Random – Seal ID	2.82e-07			
(c) *Dive residual*				
Fixed – Intercept		4.471	1.009	2.492, 6.451
non-hARS		-6.255	0.288	-6.820, -5.689
Random – Seal ID	11.55			
(d) *Duration dive vARS*				
Fixed – Intercept		3.274	0.065	3.147, 3.401
non-hARS		-0.288	0.024	-0.336, -0.240
Random – Seal ID	0.045			
(e) *Proportion dive vARS*				
Fixed – Intercept		45.793	1.280	43.283, 48.303
non-hARS		-6.531	0.185	-6.894, -6.169
Random – Seal ID	19.39			
N_{dives} = 74 834			N_{seals} = 12	

N_{dives}, number of individual dives; N_{seals}, number of individual seals; SE, standard error; 95% CI, 95% confidence interval.

Table S2. **Results of mixed models examining the effects of region and month on the dive behaviour and foraging effort of female Antarctic fur seals. (a-e)** Linear Mixed Models (LMM) were fitted to dive residual and the proportion dive vARS, while Generalised Linear Mixed Models (GLMMs) were fitted to maximum dive depth, dive duration and duration dive vARS. **(f)** Results for the best available GLMM examining the relationship between dive effort, region and month. **(g)** Results for the best available GLMM examining the relationship between foraging hours, region, month, maximum depth, dive residual, proportion of dive in vARS and night length. In all cases, the best available model was determined using delta AIC and Akaike weights and the intercept is Region N of PF and Month April.

Parameter[a]	**Variance**	**Estimate**	**SE**	**95% CI**
(a) *Maximum dive depth*				
Fixed – Intercept		2.92e-02	1.54e-03	2.64e-02, 3.23e-02
Region PF		1.25e-04	2.29e-04	-3.24e-04, 5.75e-04
Region S of PF		-1.82e-02	2.83e-04	-1.76e-02, -1.87e-02
Month May		-5.76e-04	1.64e-04	-2.53e-04, -8.98e-04
Month June		-5.94e-03	2.61e-04	-5.43e-03, -6.45e-03
Month July		-9.19e-03	2.96e-04	-8.61e-03, -9.77e-03
Month August		-6.91e-03	2.71e-04	-6.38e-03, -7.45e-03
Random – Seal ID	9.86e-06			
(b) *Dive duration*				
Fixed – Intercept		9.43e-03	2.87e-04	8.86e-03, 9.99e-03
Region PF		-7.82e-04	5.25e-05	-6.79e-04, -8.85e-04
Region S of PF		-3.59e-03	5.29e-05	-3.49e-03, -3.70e-03
Month May		1.11e-04	3.79e-05	1.85e-04, 3.67e-05
Month June		3.92e-04	5.04e-05	4.91e-04, 2.93e-04
Month July		1.02e-03	5.28e-05	1.12e-03, 9.20e-04
Month August		1.29e-03	5.21e-05	1.23e-03, 1.02e-03
Random – Seal ID	1.55e-07			
(c) *Dive residual*				
Fixed – Intercept		-0.284	1.675	-3.567, 2.999
Region PF		-8.277	0.443	-9.147, -7.407
Region S of PF		-12.873	0.394	-13.646, -12.101
Month May		2.642	0.328	1.998, 3.285
Month June		12.851	0.426	12.016, 13.687
Month July		26.183	0.481	25.238, 27.127
Month August		26.175	0.482	25.228, 27.121
Random – Seal ID	32.79			
(d) *Duration dive vARS*				
Fixed – Intercept		2.31e-02	9.51e-04	2.12e-02, 2.49e-02
Region PF		-5.56e-03	3.31e-04	-4.91e-03, -6.21e-03
Region S of PF		-9.18e-03	3.01e-04	-8.59e-03, -9.77e-03
Month May		1.35e-03	2.27e-04	1.80e-03, 9.11e-04
Month June		4.98e-03	2.83e-04	5.53e-03, 4.42e-03
Month July		7.97e-03	2.852e-04	8.53e-03, 7.41e-03

Month August		7.54e-03	2.88e-04	8.11e-03, 6.98e-03
Random – Seal ID	2.89e-06			
(e) *Prop. dive vARS*				
Fixed – Intercept		40.292	0.988	38.356, 42.229
Region PF		-5.107	0.291	-5.677, -4.537
Region S of PF		-0.895	0.258	-1.402, -0.388
Month May		1.369	0.215	0.947, 1.791
Month June		6.440	0.279	5.892, 6.988
Month July		11.949	0.316	11.329, 12.568
Month August		9.289	0.316	8.669, 9.910
Random – Seal ID	11.34			
N_{dives} = 74 008			N_{seals} = 12	
(f) *Diving hours*				
Fixed – Intercept		0.354	0.081	0.195, 0.513
Region PF		-0.399	0.070	-0.261, -0.538
Region S of PF		-0.718	0.066	-0.589, -0.848
Month May		-0.086	0.028	-0.031, -0.141
Month June		-0.108	0.039	-0.031, -0.186
Month July		-0.128	0.042	-0.045, -0.210
Month August		-0.105	0.039	-0.028, -0.182
Random – Seal ID	0.075			
(g) *Foraging hours*				
Fixed – Intercept		-0.039	0.190	-0.413, 0.333
Dive residual		-0.227	0.049	-0.323, -0.131
Maximum depth		0.796	0.052	0.694, 0.899
Night length		-0.157	0.078	-0.310, -0.004
Prop. dive vARS		1.051	0.051	0.950, 1.151
Region PF		-0.390	0.116	-0.618, -0.163
Region S of PF		-0.354	0.147	-0.643, -0.065
Month May		-0.399	0.012	-0.637, -0.161
Month June		-0.349	0.175	-0.692, -0.006
Month July		-0.731	0.164	-1.054, -0.409
Month August		-0.434	0.168	-0.763, -0.104
Random – Seal ID	0.187			
N_{nights} = 899			N_{seals} = 12	

[a]PF, Polar Front; S of PF, south of Polar Front; Prop. dive vARS, proportion of the dive in vertical area-restricted search behaviour; N_{dives}, number of individual dives; N_{nights}, number of individual nights; SE, standard error; 95% CI, 95% confidence interval.

Chapter 4

Winter habitat predictions of a key Southern Ocean predator, the Antarctic fur seal (*Arctocephalus gazella*)

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Abstract

Quantification of the physical and biological environmental factors that influence the spatial distribution of higher trophic species is central to inform management and develop ecosystem models, particularly in light of rapid atmospheric and ocean system changes. We used tracking data from 184 female Antarctic fur seals (*Arctocephalus gazella*) to develop habitat models for three breeding colonies for the poorly studied Southern Ocean winter period. Habitat models were used to identify and predict the broadly important winter foraging habitat and to elucidate the environmental factors influencing these areas. Model predictions closely matched observations and several core areas of foraging habitat were identified for each colony, with notable areas of inter-colony overlap suggesting shared productive foraging grounds. Seals displayed clear choice of foraging habitat, travelling through areas of presumably poorer quality to access habitats that likely offer an energetic advantage in terms of prey intake. The relationships between environmental predictors and foraging habitat varied between colonies, with the principal predictors being wind speed, sea surface temperature, chlorophyll a concentration, bathymetry and distance to the colony. The availability of core foraging areas was not consistent throughout the winter period. The habitat models developed in this study not only reveal the core foraging habitats of Antarctic fur seals from multiple colonies, but can facilitate the hindcasting of historical foraging habitats as well as novel predictions of important habitat for other major colonies currently lacking information of the at-sea distribution of this key Southern Ocean predator.

Introduction

Information on the spatial distribution of marine predators is fundamental to understanding the structure and function of their ecosystems and is ultimately driven by the availability of prey resources that are heterogeneously dispersed in space and time (Russell *et al.* 1992). The abundance of marine prey is intrinsically linked to physical and biological oceanographic properties, allowing us to relate the distribution and responses (such as breeding success) of higher trophic species with the fundamental bio-physical aspects of their environment (e.g. Reid & Croxall 2001; Friedlaender *et al.* 2006). Quantifiable understanding of these factors is necessary to inform and appraise management decisions such as defining marine protected areas (Hyrenbach *et al.* 2000), fisheries management and by-catch mitigation measures (Burger & Shaffer 2008), as well as for the development of accurate ecosystem models to assess the effects of future environmental changes.

The Antarctic fur seal (*Arctocephalus gazella*, Peters, 1875) is a highly mobile marine predator that inhabits an extremely dynamic environment, the Southern Ocean. Antarctic fur seals are major consumers in the Southern Ocean ecosystem, in particular of krill (Croxall *et al.* 1985) often competing with other predators such as penguins and whales for this resource (Barlow *et al.* 2002; Blanchet *et al.* 2013). Antarctic fur seals breed at 10 major sites in the Southern Ocean across their circumpolar range (Shirihai 2002), spanning latitudes from the northernmost colony at the Crozet Islands (46°25’S), north of the Polar Front, to the southernmost at the South Shetland Islands (62°27′S), within the zone of winter sea ice. The at-sea habitat use of Antarctic fur seals reflects these geographical differences and the species exhibits a diverse foraging ecology across their range, with highly flexible summer foraging behaviours within and between colonies associated with local environmental conditions (Lea *et al.* 2006) and differences in prey (Boyd *et al.* 1994; Lea *et al.* 2008; Staniland *et al.* 2010).

During the winter, non-breeding animals are free from the constraints of central place foraging (Orians & Pearson 1979) associated with provisioning their offspring. Consequently, female Antarctic fur seals can make wide-ranging migrations (Boyd *et al.* 2002) of up to eight months. Moreover, the Southern Ocean in winter is both physically and biologically distinct from the summer, with the growth of sea ice, decline in primary productivity due to decreased irradiance and temperature (Clarke 1988; Mitchell *et al.* 1991) and a deeper mixed-layer depth because of strong winds (Sakshaug *et al.* 1991), being major distinctions. Consequently, foraging animals, and their prey, can be expected to behave differently during this time. Female Antarctic fur seals are also gestating during winter (Boyd 1996) requiring them to make judicious foraging choices to maximise their energy intake in the pre-breeding period. Recent studies of the winter migrations of female Antarctic fur seals show they utilise a variety of habitats during this time, occupying all inter-frontal zones from pole-ward of the Antarctic Circumpolar Current, including ice associated waters, to north of the sub-Antarctic Front, incorporating both shelf and pelagic habitats (Boyd *et al.* 2002; Staniland *et al.* 2012).

The variety of foraging habitats utilised by Antarctic fur seals during the winter is reflected in their diet, with differences in the trophic position of their prey between the various inter-frontal zones, both within and between individuals (Walters 2014). Some female fur seals are also highly faithful to winter foraging grounds returning to the same broad foraging area annually, presumably because of an increased energy acquisition associated with these habitats over the long-term (Arthur *et al.* 2015). The diversity of habitats used by Antarctic fur seals during the winter suggests that breeding colony location is a key factor in determining the suite of habitat types available for foraging (Mary-Anne Lea, unpublished data). However, despite being a major predator in the Southern Ocean, the at-sea behaviour of Antarctic fur seals outside the breeding season remains poorly understood. In particular, little is understood about the relationships between marine characteristics and foraging behaviour and how animals from different populations respond to these factors.

Habitat models (or Species Distribution Models) can assist with this process and are often used to describe the environmental drivers of species distribution patterns, providing useful ecological insights (Elith & Leathwick 2009). Ultimately, they may be used to make predictions of species distributions in un-sampled areas or under changing environmental conditions, and have been employed across a variety of taxa, scales and environments using a range of methodologies (Guisan & Zimmermann 2000). The fundamental information on the distribution of marine predators that is needed to build such models is often provided by telemetry studies. However, these studies are often restricted to a single site or season. For Antarctic fur seals, Guinet *et al.* (2001) developed a probabilistic model for the distribution of diving activity of lactating seals at Îles Kerguelen, which predicted where animals should concentrate their foraging based on the oceanographic conditions within that year. The authors note that studies conducted over several years will provide further insights into the effects of oceanographic conditions on the foraging ecology and at-sea distribution of this, and other, marine predator species.

Here, we examine the at-sea distribution and foraging habitats of female Antarctic fur seals from three breeding colonies across multiple inter-breeding periods in the Atlantic and Indian sectors of the Southern Ocean. The study aims to: (1)

identify important foraging habitats for Antarctic fur seals during the non-breeding, winter season, (2) describe the environmental factors that characterise these areas and compare these relationships between animals from three major breeding populations and (3) develop predictive models for foraging habitat.

Materials and methods

STUDY SITES AND INSTRUMENTATION

The study was conducted at three Antarctic fur seal breeding colonies: Marion Island (46°54'S, 37°44'E, Prince Edward Islands), Bird Island (54°00'S, 38°03'W, South Georgia) and Cape Shirreff (62°27′S, 60°47′W, South Shetland Islands) (Fig. 4.1). At Marion Island, the study was undertaken over five years between 2008 and 2013, at Bird Island for four years between 2008 and 2011 and at Cape Shirreff for three years between 2008 and 2010. Adult females were captured towards the end of lactation between February and April and were instrumented with a global-location sensing (GLS; British Antarctic Survey, Cambridge UK) logger for the duration of their winter migrations. Seals were recaptured and instruments recovered at the start of the following breeding season in November-December when pregnant females return to the colony to pup. Several animals were recaptured in subsequent years. Animal handling, GLS logger architecture, attachment and calibration methods are detailed in Arthur *et al.* (2015).

TRACKING DATASETS

Locations were produced from the raw light and temperature data from GLS loggers following the Bayesian approach of Sumner et al. (2009) using the R software

(R Core Team 2014) package 'tripEstimation' (Sumner & Wotherspoon 2010). In summary, two location estimates per day (each representing a 12-hour period centred on dawn and dusk) were produced from the posterior mean for each twilight period that were summarised from the accepted Markov Chain Monte Carlo (MCMC) samples. Full details of geo-location model design and implementation are presented in Supporting Information S1. Seals undertook between 1-9 foraging trips per winter with the average ± SD being 2.2 ± 1.5 at Marion Island, 2.5 ± 1.6 at Bird Island, while all animals at Cape Shirreff undertook a single trip. For animals making multiple foraging excursions from their colony, tracks were split into individual trips and analysed independently. Individual trips were identified in the raw light data, with haul-outs typified by distinctly messy light curves resulting from the animal periodically shading the light sensor while on land. Winter foraging trips encompassed the first post-weaning excursion (typified by a marked increase in duration from short trips during lactation) to the animal's return to the colony the following breeding season. Between 2008-13, 184 GLS tags were recovered from post winter migrations across the three colonies (Table 4.1). Unprocessed GLS data are publicly available from the Australian Antarctic Data Centre (http://data.aad.gov.au) for each site: Marion Island (Lea *et al.* 2014a), Bird Island (Lea *et al.* 2014c) and Cape Shirreff (Lea *et al.* 2014b).

HABITAT MODELS

Models were constructed to explain the spatial distribution of Antarctic fur seal habitat use during the winter. The mean time spent in each cell (total time spent divided by the number of seals visiting each cell) of a 60 km x 60 km grid consistent across the spatial extent of locations (Table 4.1) was calculated for the period of study to quantify habitat use, hereto referred to as *time spent*. As nearly all animals were tracked for the same amount of time during their winter migrations, total time spent, rather than a proportion, was used. A grid of this resolution was chosen to match the error uncertainty surrounding geo-location estimates, which is shown to be 70 ± 35 km for an Antarctic fur seal carrying GLS and Argos tags simultaneously (Mary-Anne Lea, unpublished data). Time spent is a proxy for foraging effort as animals are likely to spend more time in an area which they are actively exploiting than when travelling between foraging areas (Kareiva & Odell 1987; Barraquand & Benhamou 2008). Time spent was a continuum from low to high use and can be considered a "usage" approach, being similar to kernel density analysis often applied to tracking data, rather than as a binary presence-absence response contrasting areas where animals did go with areas that they didn't go. Three winter habitat models were generated: one for each colony with data pooled across all available years. Prior to developing these models, an assessment of the adequacy of the sample size at each colony was undertaken. We assessed the amount of new information (i.e. grid cells) arising from the inclusion of each additional individual seal (averaged over 100 permutations), providing an estimate of the minimum number of individuals needed to adequately represent the spatial distribution patterns of animals from each colony.

Environmental parameters

A suite of environmental variables that potentially influenced time spent was included in models to characterise fur seal habitat. Variables were chosen for a priori reasons based on our understanding of the nature of the variables and how they relate to the biology of the seals. Variables included static parameters: bathymetry (BATHY) and distance to colony (d2col) and dynamic parameters: sea surface temperature

(SST), sea surface height anomaly (SSHa), chlorophyll a concentration (CHLa), wind speed, surface current magnitude (CURR) and eddy kinetic energy (EKE). Variability of sea surface height anomaly (SSHV) and the gradient of sea surface temperature (SSTG) were also included (Fig. 4.1). The source, spatial resolution and oceanographic significance of environmental variables are provided in Table A1. Environmental data were extracted for each pixel of the spatial domain at weekly intervals spanning the temporal range of location data at each colony. The grid-based approach aggregated tracking data over multiple years, so weekly environmental variables were averaged to produce a mean parameter value per cell for the period of study (in the case of SSHV variance was calculated) to create a temporal climatology (Sumner *et al.* 2003). These climatologies allow investigation of the influence of environmental factors on seal habitat use across broad spatial and temporal scales. All variables were re-interpolated across a 60 km x 60 km grid to match the time spent response data. All data, including environmental predictors and time-spent response, were then re-projected to Lambert azimuthal equal-area projection. Environmental data were available from the Australian Antarctic Data Centre and extracted using the R package 'raadtools' (Sumner 2015).

Model design and predictions

Generalized additive models (GAMs) were fitted to the relationship between time spent and environmental climatology predictors. To determine the most appropriate error structure, a comparison was made between Gaussian models with an identity link, log-transformed Gaussian with identity link, and Gamma with a log link models. Log-likelihood and Akaike's Information Criterion (AIC) scores adjusted to account for transformation were used for model comparison and to determine the most appropriate error structure. The distribution of environmental predictors was examined and data were log-transformed where appropriate to meet the assumptions of normality. For numerical stability, predictors were scaled and centred to account for the considerably different scales of measurement. Highly correlated predictor variables (Pearson's $r > 0.9$) were excluded from the model build. Model selection was undertaken using the maximum-likelihood approach to minimise the AIC. Models including all combination of variables were compared and ranked by their Akaike weight (*w*AIC) to represent the relative likelihood of each model.

To account for individual variability in the response term, it is possible to include a random term in the GAM framework (Wood 2006). However, such models are computationally demanding and potentially problematic for smaller relative sample sizes (Raymond *et al.* 2014), so standard GAMs were utilised. The influence of individual variability was instead reduced by using the average value of time spent across trips in each cell. A further problem arises with tracking data that are spatially auto-correlated, which can lead to violations of the assumption of independence of residuals. We therefore included an autocovariate term in all models (Wood 2006).

Model performance was evaluated by assessing model fit and predictive performance. Model fit was indicated by the percent deviance explained and by checking model residuals. The predictive performance of models was assessed by calculating the root mean-squared error (RMSE) using a k-fold cross-validation procedure. Grid cells were randomly assigned to one of 10 folds where models were trained on nine folds and tested on the remaining one, with each fold withheld in turn. The RMSE (expressed in the same units as the response) was aggregated across the 10 sets of results. The best model for each population was then fit on the unscaled and uncentred environmental predictor variables with the sole purpose of aiding the interpretability of the smoothed relationships on meaningful scales. Lastly, models were used to predict winter habitat use of fur seals by interpolating across the entire spatial domain of the locations observed for each colony. This necessitated extrapolating in environmental space, notably for the northern and southern range extents. All analyses were conducted in R 3.2.0 (R Development Core Team).

Table 4.1. Summary of data: Number of tags deployed, recovered, trips recorded and locations estimated by site and year collected for the winter foraging trips of female Antarctic fur seals.

Site	Year	GLS deployed	GLS recovered	N trips	N locations	Spatial extent of locations	
						Latitude	Longitude
Marion Island	2008	30	20	42	9035		
	2009	31	10	27	6509		
	2010	16	8	17	3148		
	2011	42	32	71	13 588		
	2012	30	26	41	16 709		
	2013	30	23	28	5062		
	All years	*179*	*119*	*227*	*54 051*	*41.4°S to 65.0°S*	*0.1°E to 69.3°E*
Bird Island	2008	29	3	6	1407		
	2009	30	9	18	4665		
	2010	30	10	21	4186		
	2011	30	6	11	2070		
	All years	*119*	*28*	*56*	*12 328*	*41.7°S to 68.5°S*	*71.3°W to 4.7°W*
Cape Shirreff	2008	18	14	14	6562		
	2009	19	11	11	5309		
	2010	19	12	12	5546		
	All years	*56*	*37*	*37*	*17 417*	*41.3°S to 69.6°S*	*136.1°W to 35.6°W*
Total		**354**	**184**	**320**	**83 796**		

Results

DISTRIBUTION OF TIME SPENT IN AREA

Between 2008-13, a total of 320 foraging trips and 83 796 location estimates were observed for 184 female Antarctic fur seals during the austral winter. At Marion Island, 54 051 locations from 227 trips were available for 119 female seals with 12 328 locations from 56 trips and 28 seals at Bird Island, and 17 417 locations across 37 trips collected for 37 animals from Cape Shirreff (Table 4.1, Fig. A1). For Marion Island, the cumulative information curve showed that the number of newly visited grid cells arising from the inclusion of each additional animal asymptotes at approximately 50 individuals (Fig. 4.2c), indicating we had an adequate sample to accurately represent the spatial use patterns of the population. The curve for Bird Island closely matched that of Marion Island, however it failed to level out completely, suggesting that additional animals would better represent the distribution patterns of this population. Similarly, at Cape Shirreff, 37 animals were observed and although the curve is beginning to asymptote, it failed to level out entirely (Fig. 4.2c), indicating a greater number of animals are needed to more fully characterise the variability in habitat use for this population.

The distribution of time spent for Marion Island fur seals indicated that animals utilised a diversity of areas during their winter migrations (Fig. 4.3). Of prominent use were areas located approximately 100-800 km to the north and east of Marion Island associated with the Del Cano Rise, and pelagic waters to the west of the island between 20-30°E. Time spent values were also high in several areas to the south of the colony at approximately 55°S as well as other locations at the extreme east and west of the population's range, notably around Bouvet Island and east of Iles Kerguelen. Seals spent relatively little time in local waters within several hundred kilometres to the west and south of Marion Island, suggesting animals transited through these areas to reach distant foraging grounds.

For the Bird Island population, time spent was concentrated mostly in local waters within approximately 300 km of South Georgia, particularly to the northwest of the colony (Fig. 4.3). There was a further area of high usage to the south of South Georgia. Additional high-use areas were off the Patagonian coast of South America, east of South Georgia towards the Scotia Arc and South Sandwich Islands and on the continental shelf along the western Antarctic Peninsula.

At Cape Shirreff, the areas of high usage were along the southern coast of Chile associated with the shelf-break and pelagic waters further west of this region (Fig. 4.3), and waters to the west of South Georgia. Time spent values were high along the Patagonian shelf-break and several distant pelagic areas at the western extent of the population’s range (westward of 110°W longitude) resulting from individual animals concentrating their efforts in these regions for extended periods.

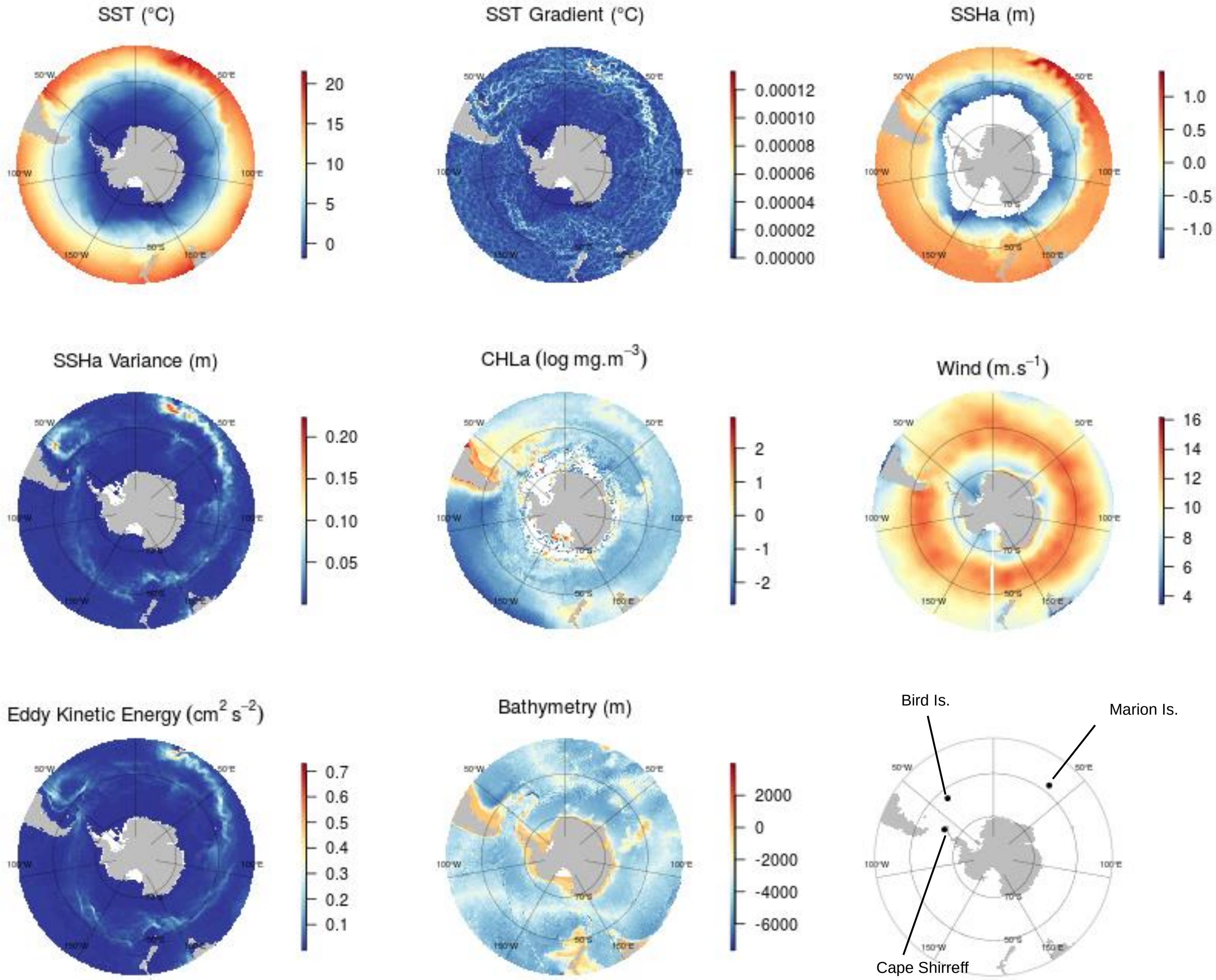

Figure 4.1. Maps of eight environmental climatology variables likely to influence fur seal foraging effort during the Southern Ocean winter (April-December). Variables were averaged across all winters in the study period (2008-13), except for SSHa Variance, for which variance was calculated. The location of the three study colonies are shown on the map in the bottom right panel.

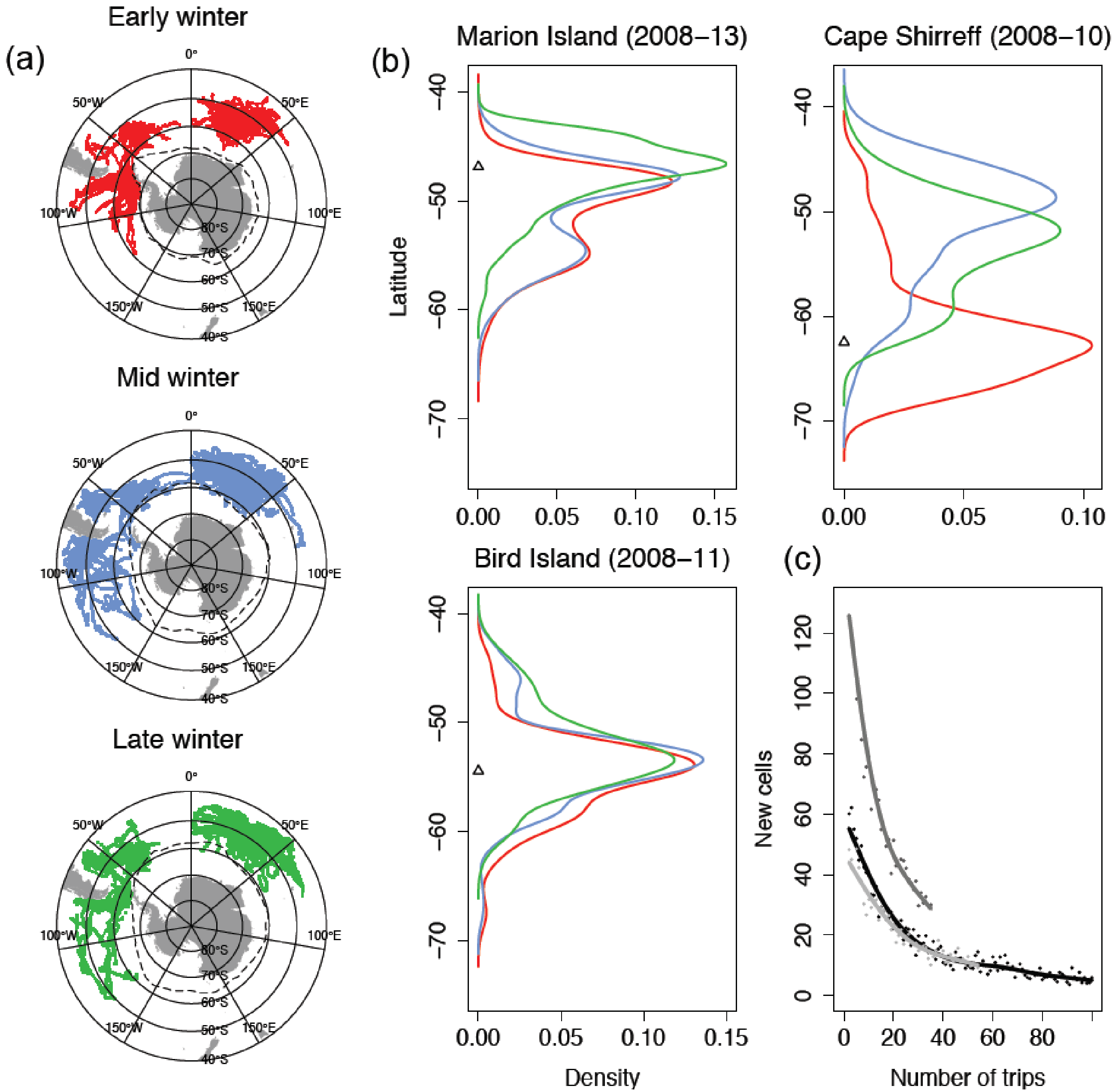

Figure 4.2. (a) Winter tracks for female Antarctic fur seals (n=184) split into three periods: early (March-May), mid (June-August) and late (September-December) winter. The mean sea ice extent for each period over the five years (2008-13) is represented by the dashed lines. **(b)** Density distribution of locations by latitude of fur seals from Marion Island (n=119), Bird Island (n=28) and Cape Shirreff (n=37) during early (red), mid (blue) and late winter (green). Triangles show the latitude of each colony. **(c)** The average number of new grid cells visited with the inclusion of additional foraging trips for the Marion Island (black), Bird Island (light grey) and Cape Shirreff (dark grey) colonies.

ENVIRONMENTAL CHARACTERISTICS OF HIGH-USE AREAS

Across the spatial distribution of all three populations, EKE and CURR oceanographic variables were highly correlated ($r > 0.95$). Eddy fields associated with larger current systems can be important to foraging predators (Bailleul *et al.* 2010), so CURR was subsequently excluded from analyses, leaving nine predictor variables available for model build. For the Marion Island population, the best model explaining mean time spent in a grid cell included all variables but SSTG (*w*AIC = 0.691; Table 4.2) fit to a Gamma error structure. Model residuals were normally distributed and the model explained 73.3% of the deviance in the data and had good predictive performance ($r^2 = 0.704$, RMSE = 14.30). Omitting the spatial autocorrelation term from the model still produced good model fit ($r^2 = 0.413$, RMSE = 19.93), suggesting the broad relationships between time spent and environmental variables were robust. The strongest relationships between foraging effort and the seals' environment were observed with Wind, SST, SSHV and d2col. Antarctic fur seals from Marion Island spent more time, on average, in areas of higher wind speeds (>12 $m.s^{-1}$) with greater SSHV. Seals preferred water temperatures that were either colder (~0ºC) or warmer (between 6ºC and 10ºC) than average and areas that were further (>1500 km) from the colony (Fig. 4.4a).

The best model for the Bird Island population was a reduced Gamma model excluding CHLa and SSHV (*w*AIC = 0.355; Table 4.2). Model assessment suggested a good fit to the observed data with the model explaining 85.3% of the deviance in the data and having good predictive performance ($r^2 = 0.828$, RMSE = 13.24). Model performance was good when the spatial autocorrelation term was excluded ($r^2 = 0.591$, RMSE = 19.76). The clearest relationships with time spent were with BATHY, Wind and d2col. These indicated that cells close to the colony (<500 km), with shallow relative water depths (<2000 m) and with lower wind speeds (<10 m.s^{-1}) had high mean time spent values (Fig. 4.4b).

At Cape Shirreff, the best model explaining time spent was a Gamma model excluding SSTG and BATHY predictor terms (*w*AIC = 0.594; Table 4.2). Model residuals and cross validation indicated the model was a good fit to the observations, explaining 72.5% of the deviance in the data (r^2 = 0.701, RMSE = 15.63). Model performance was good when the spatial autocorrelation structure was omitted (r^2 = 0.461, RMSE = 20.55). The strongest relationships between mean time spent and environmental predictors were for d2col, Wind and SST. The smoothed relationships indicated that seals from Cape Shirreff spent more time in areas of colder (between -1ºC and 5ºC) or warmer (>10ºC) than average water temperatures and with and high relative wind speeds (>10 m.s^{-1}) when closer to the colony (Fig 4.4c).

Table 4.2. Summary of generalised additive model (GAM) comparisons examining the relationship between foraging effort (time spent per grid cell) and environmental variables for: (a) Marion Island, (b) Bird Island and (c) Cape Shirreff colonies. TS = time spent, SST = sea surface temperature, SSTG = sea surface temperature gradient, SSHA = sea surface height anomaly, SSHV = sea surface height variance, Wind = wind speed, CHLa = chlorophyll a concentration, BATHY = bathymetry, d2col = distance to colony, (lon,lat) = spatial autocorrelation term. Only models with a **Δ**AIC <10 are shown and the accepted model is presented in bold.

Candidate models	*k*	LL	AIC	ΔAIC	*w*AIC
(a) Marion Island					
1. **TS ~ SST + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)**	**10**	**-24833.0**	**49851.2**	**0.0**	**0.691**
2. TS ~ SST + SSTG + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	11	-24832.5	49852.9	1.7	0.295
3. TS ~ SST + SSHA + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)	9	-24843.5	49859.1	7.9	0.013
(b) Bird Island					
1. **TS ~ SST + SSTG + SSHA + Wind + BATHY + EKE + d2col + (lon,lat)**	**9**	**-13702.8**	**27563.4**	**0.0**	**0.355**
2. TS ~ SST + SSTG + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	11	-13695.9	27563.5	0.1	0.334
3. TS ~ SST + SSTG + SSHA + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	10	-13702.1	27563.8	0.4	0.291
4. TS ~ SST + SSTG + SSHA + Wind + EKE + d2col + (lon,lat)	8	-13706.8	27569.3	5.9	0.017
(c) Cape Shirreff					
1. **TS ~ SST + SSHA + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)**	**9**	**-27232.9**	**54637.4**	**0.0**	**0.594**
2. TS ~ SST + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	10	-27232.9	54638.9	1.5	0.287
3. TS ~ SST + SSTG + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	11	-27232.8	54640.7	3.3	0.115

k, number of parameters; LL, log-likelihood; AIC, Akaike's Information Criterion; **Δ**AIC, difference in AIC from that of the best fitting model; *w*AIC, AIC weight; prop dive vARS, proportion of the dive in vertical area-restricted search behaviour.

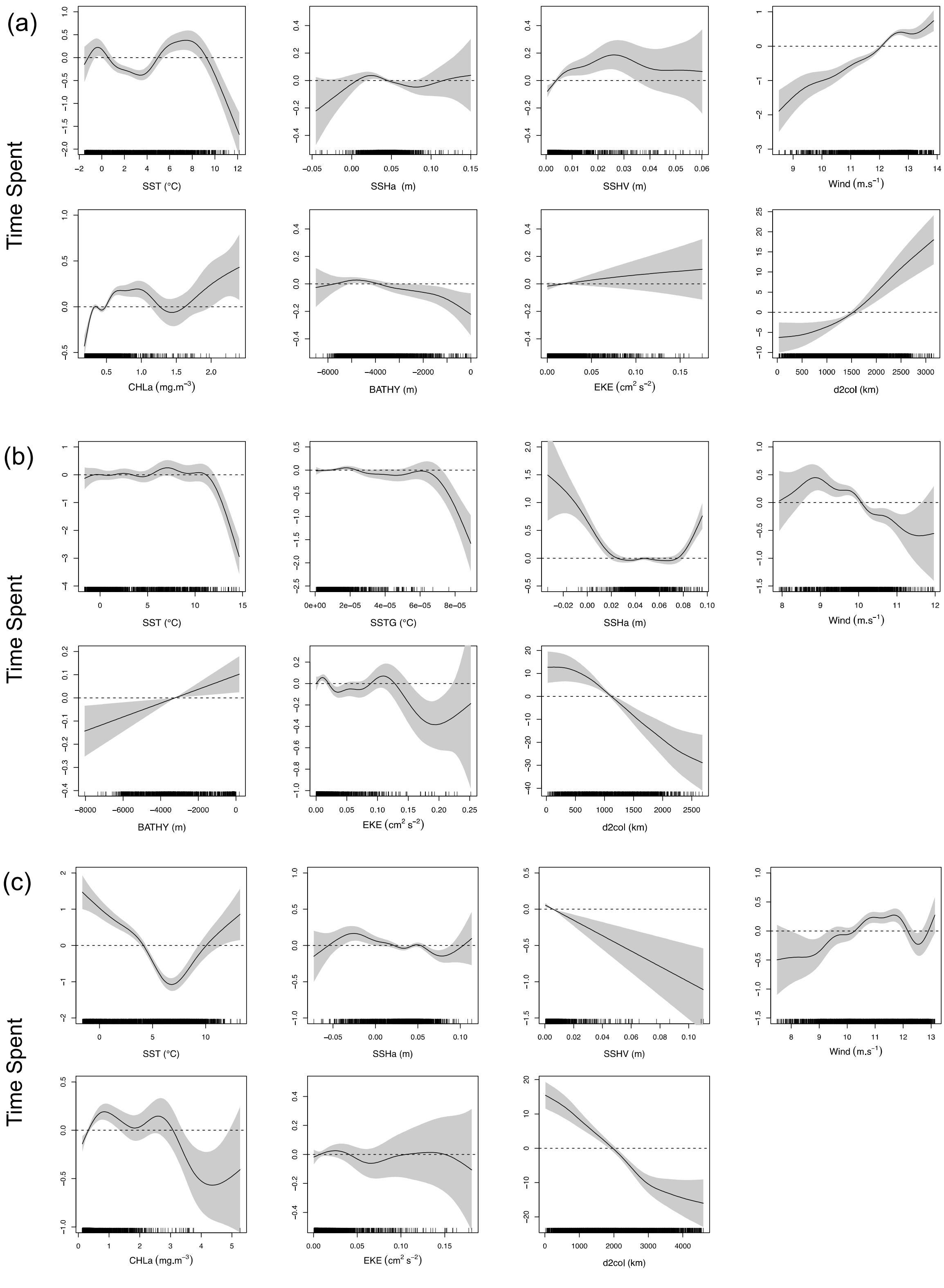

Figure 4.4. Predicted time spent per grid cell in relation to key environmental parameters (unscaled and uncentred) for the winter foraging effort of female Antarctic fur seals. Lines show the prediction of a GAM fit to a Gamma error structure for (a) Marion Island, (b) Bird Island and (c) Cape Shirreff. Shading represents the 95% confidence interval for predictions. Black bars show the distribution of observations. SST = sea surface temperature, SSTG = sea surface temperature gradient, SSHa = sea surface height anomaly, SSHV = sea surface height variance, Wind = wind speed, CHLa = chlorophyll a concentration, BATHY = bathymetry, d2col = distance to colony.

PREDICTING IMPORTANT WINTER FORAGING HABITAT

The habitat models were interpolated across the entire spatial domain of observations from each population. The resultant distribution maps of winter foraging habitat are shown in Figure 4.3. For all three populations these predictions closely matched the time-spent observations recorded in this study, giving us further confidence in the ability of the models to make realistic predictions of important foraging habitat for Antarctic fur seals in the different oceanic basins. For seals from the Marion Island colony, the model successfully predicted the major areas of observed time spent, being those regions to the east, west and far south of the colony. At Bird Island, likely important foraging habitat was identified in waters local to South Georgia and extending south, as well as on the Patagonian Shelf, north of the Scotia Arc and the West Antarctic Peninsula, closely matching observations. Newly predicated habitat was located north of Tierra del Fuego (southern tip of South America) and at the extreme eastern edge of the range of tracked animals, however, we note this is driven by observations from a single animal only. The Cape Shirreff model predictions also closely matched the observations, with the model identifying the three major focal areas for animals from this population: the southern Chilean coast, the Patagonian Shelf break and around South Georgia. Notably, additional important foraging habitats were predicted for coastal waters on the Patagonian Shelf and oceanic waters around 100°W longitude at the northern extent of the population's range, which were areas with no previous observations and likely involved extrapolation in environmental space.

Predicted important foraging habitats were not wholly distinct between the three populations, with clear overlap of some areas (Fig. 4.3). Seals from Cape Shirreff and Bird Island in particular, have considerable overlap in their predicted use of habitats around South Georgia, along the Patagonian Shelf and, to a lesser degree, waters of the western Antarctic Peninsula. Important foraging habitat around Bouvet Island in the Southern Atlantic sector is also likely to be shared by the Bird and Marion Island populations.

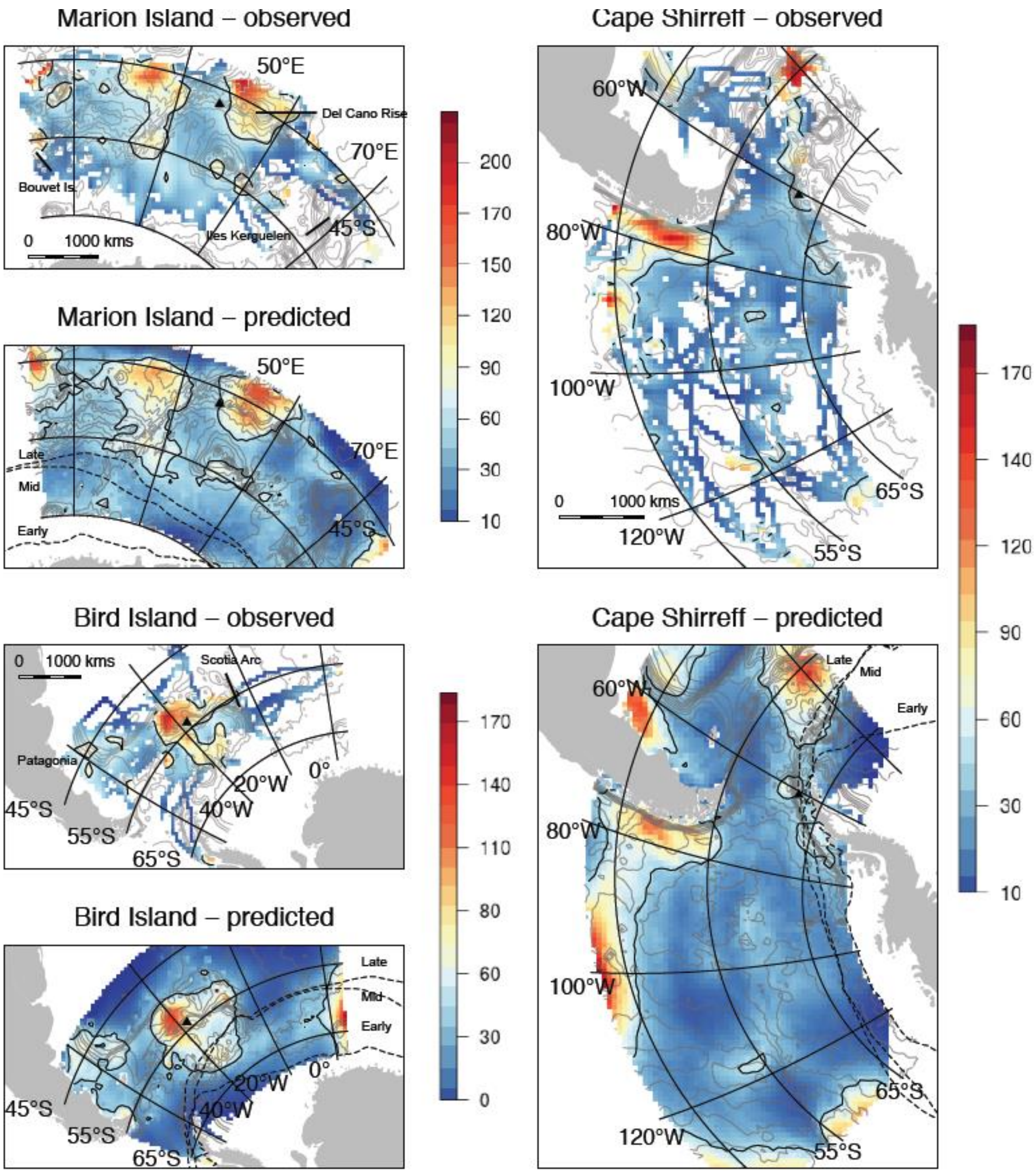

Figure 4.3. Observed and predicted winter habitat use (time spent in hours per cell of a 0.6° x 0.6° grid) for female Antarctic fur seals from Marion Island, Bird Island and Cape Shirreff. The 75% distribution areas are shown by solid black lines. Dashed lines show the average position of the sea ice edge for early, mid and late winter. Black triangles show the location of each colony.

Discussion

Our study considers time spent as a proxy for foraging effort in Antarctic fur seals. Residence time is a suitable proxy as an animal is likely to spend more time in an area that it is actively exploiting (area-restricted search) than when travelling between foraging areas (Barraquand & Benhamou 2008) and several studies have shown high relative residence times to be associated with increased dive effort and food intake in marine predators (Cotté *et al.* 2007; Thums *et al.* 2008), including Antarctic fur seals (Arthur *et al.* 2016). We therefore refer to foraging habitat and effort henceforth.

By using tracking data from multiple sites in the Southern Ocean across several years this study has revealed the broadly important foraging habitats, and the environmental conditions that characterise these, for female Antarctic fur seals during the poorly studied winter period. During that time, when animals are free to range widely, there are several habitats that are important for seals. The performance of habitat models was good, with predictions interpolated across the spatial domain of each population closely matching the observed data. The models also identified several novel areas of importance where no animals had been observed, particularly for the Cape Shirreff population. However, some of these areas likely involved predictions from extrapolating in environmental space, particularly at the northern and southern range extents, and their significance should be interpreted with caution. The cumulative information analysis suggested the minimum number of animals needed to adequately characterise the spatial use patterns of this population was not achieved, unlike at Marion and Bird Islands, where little novel habitat was predicted. We are therefore confident in the ability of the habitat models to make realistic predictions of the foraging habitat for this species.

Habitat models can perform well in characterizing the distribution of species within their current range and spatial interpolation is generally reliable providing data and model design are reasonable (Elith & Leathwick 2009). Habitat modelling has been used to quantify species-environment relationships and predict the distributions of a variety of taxa including terrestrial and aquatic plant species, terrestrial animal species, fish, plant communities, vegetation types and biodiversity (For reviews see Guisan & Zimmermann 2000; Guisan & Thuiller 2005). More recently, habitat models have been applied to marine species, including highly mobile top predators in an effort to identify critical oceanic habitats (e.g. Block *et al.* 2011) including for the Southern Ocean (Hindell *et al.* 2011; Raymond *et al.* 2014).

For the three Antarctic fur seal populations in this study, distinct foraging areas were identified for the winter period. At Marion Island, core foraging areas were contiguous with the Del Cano Rise, a prominent bathymetric feature associated with the development of eddies and spring/summer phytoplankton blooms (Pollard *et al.* 2007; Venables *et al.* 2007) known to be utilised by foraging predators from Marion Island (de Bruyn *et al.* 2009). Further core habitat was to the west of the colony and south towards the Polar Front, a region of focus for several apex predator species because of the predictable distribution of prey such as mesopelagic fish (Bost *et al.* 2009). At Bird Island, core habitat was located in the productive waters around South Georgia and downstream, where zooplankton biomass is approximately four to five times higher than in other typical Southern Ocean areas (Atkinson *et al.* 2001), as well as on the Patagonian Shelf which is an important winter foraging region for other predators from South Georgia such as white-chinned petrels (*Procellaria aequinoctialis*, Linnaeus, 1758) (Phillips *et al.* 2006). These results broadly match those of the only other studies of the winter movements of Antarctic fur seals from

South Georgia (Boyd *et al.* 2002; Staniland *et al.* 2012). For Antarctic fur seals from the South Shetland Islands, important habitat was located off the Chilean coast proximate to the high-primary productivity, cold Humboldt Current system and associated upwelling (Daneri *et al.* 2000) as well as the Patagonian Shelf break and around South Georgia.

The use of core foraging areas is ultimately driven by prey availability. Unfortunately, direct measurements of prey distribution have poor spatial and temporal coverage in the Southern Ocean and regional-scale models therefore rely on environmental proxies that characterise ocean processes related to prey distribution (Bost *et al.* 2009). Nonetheless, investigation of proximate drivers can aid in understanding the bio-physical properties of habitats. The environmental parameters in this study provide indices, effectively summarising the environment across years. Consequently, this limits the inferences that can be made, precluding the investigation of fine-scale spatial or temporal regional relationships. Any relationships that are identified, however, are likely to be broad and generally robust. Although the relationships between foraging effort and environmental parameters differed between populations, the principal predictors in habitat models were wind speed, sea surface temperature, distance to colony, chlorophyll a concentration and bathymetry.

Wind speed contributed strongly to all three models. Antarctic fur seals from Marion Island and Cape Shirreff foraged more in windier areas, while seals from Bird Island foraged in areas with low to moderate wind speeds, as was observed for female northern fur seals (*Callorhinus ursinus*, Linnaeus, 1758) (Sterling *et al.* 2014), a northern hemisphere analogue for Antarctic fur seals. Wind strength and associated winter storms can impact the dispersal routes of predators (Lea *et al.* 2009) and the vertical distribution of biomass, with prey driven deeper by the increased mixing and turbulence resulting from higher wind stress (Incze *et al.* 2001). Seals from Bird Island, which feed largely on lower trophic level prey such as krill (Reid & Arnould 1996), foraged more in areas of reduced wind speeds where prey fields may be higher in the water column and therefore more accessible. Conversely, at Marion Island and Cape Shirreff, seals preferred windier areas. Marion Island animals, which feed mainly on mesopelagic fish and squid in winter (Walters 2014) also foraged more in areas with higher eddy kinetic energy. Wind is important to the vertical distribution of biomass in mesoscale eddies, with zooplankton distribution typically deeper under high wind events (Mackas *et al.* 2005). Despite high winds impacting the vertical distribution of biomass the aggregation of prey in eddy features such as those along the South West Indian Ridge around Marion Island (Ansorge & Lutjeharms 2005) makes them important areas to foraging predators (Nel *et al.* 2001).

Habitat accessibility was also an important determinant of foraging habitat for Bird Island and Cape Shirreff colonies, with animals typically foraging less in areas that were relatively distant from breeding colonies, likely because of the energetic costs associated with travel. The exception was at Marion Island, where animals foraged in more distant areas. Sea surface temperature contributed highly to habitat models for Marion Island and Cape Shirreff, with animals decreasing their foraging effort in areas of average temperatures and preferring relatively cold or warmer waters. Although the use of water masses with certain temperatures by foraging predators can indicate preferences for productive oceanic features such as fronts (e.g. King penguins and the Polar Front, Péron *et al.* 2012), temperature is inherently coupled with latitude in the Southern Ocean and may simply be a product of how far north or south seals travelled during their wide-ranging migrations. Seals from Marion Island foraged more in areas of elevated average chlorophyll a concentration, supporting observations for this species during the summer season at Kerguelen Island (Guinet *et al.* 2001). The habitat model for Bird Island showed a strong positive relationship with bathymetry, indicating seals preferred to forage in the shallower waters (<2000m) of South Georgia and the Patagonian Shelf (Fig 4.1) where they feed on neritic prey (Walters 2014).

The availability of important foraging habitats to Antarctic fur seals varies throughout the winter and usage of the major habitats identified here will not be consistent throughout the winter. If the non-breeding winter season is divided into three periods: early winter (March-May), mid winter (June-August) and late winter (September-December), there are obvious differences in habitat availability.
At Marion Island, seals had a reduced longitudinal range in early winter relative to mid or late winter (Fig. 4.2a) due to their recent departure from the colony. Seals utilised more southerly regions in early and mid winter, shifting their distribution north in late winter (Fig. 4.2b), where foraging habitats east and west of the colony are likely to be exploited. At Bird Island, there were no significant variations in latitudinal range across the season (Fig. 4.2b). Fur seals from Cape Shirreff displayed a notable latitudinal shift in distribution across the winter, utilising areas between 60-65°S in early winter and more northerly habitats around 45-55°S as winter progressed (Fig. 4.2b).

The accessibility and use of foraging habitat can vary in response to factors including environmental conditions, prey availability, competition, predation risk, breeding status and age (Weimerskirch *et al.* 1993; Nakano 1995; Field *et al.* 2005; Heithaus & Dill 2006; Nordstrom *et al.* 2013). Of particular importance, is the reproductive cycle, with the early post-breeding period a critical time for recovering body condition after the extended lactation of otariid seals, which is energetically costly (Pitcher *et al.* 1998). Although animals are released from the constraints of parental care and free to travel further during this time (Lowther *et al.* 2014), predictable and profitable habitat in close proximity to breeding colonies, such as those to the east of Marion Island, around South Georgia and the Antarctic Peninsula, will be critical for fast energy acquisition. For marine predators lacking specialised adaptations, the growth of winter sea ice can represent a barrier excluding them from an area (Ainley *et al.* 2003). Although some Antarctic fur seal females are known to utilise sea-ice habitats during winter (Mary-Anne Lea, unpublished data), they are not considered an ice-obligate species and are mostly absent from areas of significant ice cover. Consequently, the availability of southerly habitats to fur seals, particularly around the Western Antarctic Peninsula and south of South Georgia, where krill is a significant dietary component (Walters 2014), is restricted to the early winter prior to the growth of sea ice (Fig. 4.2a). As ice cover excludes seals from southern regions in mid to late winter, more northerly habitats are increasingly utilised, especially for animals from Cape Shirreff where areas off the Chilean coast and around South Georgia and the Patagonian Shelf are important. We suggest that habitats close to breeding colonies and those that will be covered by winter sea ice are critical immediately after seals depart the colony in April-May, whereas regions further north will be increasingly utilised throughout mid to late winter during which time the availability and quality of food resources can strongly effect the risk of abortion (Soto *et al.* 2004) and reproductive success the following breeding season (Boyd *et al.* 1995).

The important Antarctic fur seal foraging areas identified in this study were not unique to colonies, with some areas used by seals from multiple populations. Animals from Bird Island and Cape Shirreff in particular had considerable overlap of foraging areas, as do the Bird and Marion Island populations although to a lesser degree. Furthermore, there will likely be inter-population overlap with seals from the study populations and other colonies in the Southern Atlantic and Indian Oceans including Crozet, Kerguelen, Heard, Bouvet, the South Sandwich and the South Orkney Islands. Although Antarctic fur seals are generally regarded as philopatric in respect of breeding sites (Lunn & Boyd 1991), tracking studies demonstrate the species' capacity for widespread dispersal (e.g. Boyd *et al.* 2002). It is not unexpected, therefore, that animals from multiple breeding sites will migrate to shared productive areas. Some Antarctic fur seals are highly faithful to winter foraging grounds and return to the same broad area annually (Arthur *et al.* 2015) and the pattern of inter-colony overlap may, in part, be a product of colony memory of major foraging habitats (Bonadonna *et al.* 2001).

Conclusions

When considered together, the areas identified in this study constitute the important foraging habitats that are exploited by a key Southern Ocean predator throughout the poorly studied non-breeding winter period. The broad spatial and temporal approach of this study has produced realistic estimates of the foraging habitat of Antarctic fur seals from three populations in the Southern Atlantic and Indian Oceans. Seals display clear choice of foraging habitat, travelling through regions of seemingly poorer quality habitat to access areas with probable elevated prey availability. Such areas can be several thousand kilometres from breeding colonies and consequently the seals balance energy intake with the costs of travel and prey searching (Charnov 1976).

Appreciation of the temporal shifts in availability and use of foraging habitats during this ~9 month period is important not only biologically, but also from a management context. Antarctic fur seals are currently the only pinniped indicator species contributing to the Commission for the Conservation of Antarctic Marine Living Resources' (CCAMLR) Ecosystem Monitoring Program (CEMP), which aims to manage the ecological impacts of commercial fishery harvests in the Southern Ocean. An increased understanding of the habitat use of this species is therefore critical to inform conservation management and will facilitate future investigation of the potential effects of short (i.e. El Niño Southern Oscillation and Southern Annular Mode) and long-term oceanographic changes (i.e. climate change) on the habitat use and foraging behaviour of this species.

Recently, the objective of habitat models has shifted towards documenting habitat change and extrapolating model predictions to novel areas (Elith & Leathwick 2009). The habitat models developed in this study can be used to hind cast foraging habitat, establishing historical distribution ranges that can be compared to current observations to indicate past habitat changes and improve our understanding of future distribution shifts. Such extrapolation is inherently risky because there are often no observations available to directly support the predictions (Elith & Leathwick 2009), however there is often no way around this. The development of seasonal habitat models to better elucidate the temporal variation in habitat importance over the winter will also help quantify when key foraging habitats are used by fur seals and to what degree any potential overlap with human activities such as fishing may occur. For marine predators, habitat models are a useful conservation tool to identify critical habitats of understudied populations without the need to undertake time-consuming and expensive tracking programs. Subsequently, habitat models for the three Antarctic fur seal colonies from this study can be used to predict critical foraging habitat for seals from other key Southern Ocean colonies where information on the winter at-sea distribution is currently not available. Among other considerations, information on local habitat availability and preferences will be necessary for accurate extrapolation (Torres *et al.* 2015) and careful consideration of the environmental and oceanographic similarities of model and prediction populations will be important.

Acknowledgements

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Supporting Information

Supporting Information S1. Methods section of Lea *et al.* (unpublished data) detailing the location estimation and state-space modelling procedures employed (Presented in Supporting Information Chapter 2).

Appendix A

Figure A1. **Mean estimated winter locations for foraging trips (n=320) of female Antarctic fur seals (n=184) from Marion Island (2008-13; red), Bird Island (grey; 2008-11) and Cape Shirreff (green; 2008-10).** Colony locations are shown in yellow.

Table A1. The source, spatial resolution and ecological significance of environmental predictor variables.

Variable	Source	Spatial resolution	Oceanographic process and significance
Sea surface height anomaly (SSHA)	AVISO	0.25° x 0.25°	Discrimination of water masses and fronts
Sea surface height anomaly variance (SSHV)	AVISO	0.25° x 0.25°	Mesoscale activity
Sea surface temperature variance (SST)	OISST	0.25° x 0.25°	Temperature of water masses
Sea surface temperature gradient (SSTG)	OISST	0.25° x 0.25°	Frontal activity and local convergence
Chlorophyll a concentration (CHLa)	Johnson Improved	0.083° x 0.083°	Primary production, prey availability
Wind speed (wind)	NCEP/DOE AMIP-II	2.5° x 2.5°	Storm events
Surface currents (CURR)	AVISO	0.25° x 0.25°	Mesoscale activity, currents
Eddy kinetic energy (EKE)	Derived from u and v current components*	0.25° x 0.25°	Mesoscale variability, local productivity and prey aggregation
Bathymetry (BATHY)	gebco_08	0.083° x 0.083°	Depth, discrimination of coastal and oceanic waters
Distance to colony (d2col)			Accessibility from colony

*Eddy kinetic energy calculation: EKE = ½ (CURRu^2 + CURRv^2)

Table A2. Model comparisons used to select the most appropriate error structure for GAMs for each colony. The model with the most appropriate error structure is presented in bold.

Candidate models	Error family	Link function	LL	AIC
(a) Marion Island				
1. TS ~ SST + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	Gaussian (untransformed)	Identity	-25043.8 (80.9)	50249.4
2. TS ~ SST + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)	Gaussian (log-transformed)	Identity	-24884.6 (89.6)	49868.5
3. **TS ~ SST + SSHA + SSHV + Wind + CHLa + BATHY + EKE + d2col + (lon,lat)**	**Gamma**	**Log**	**-24833.0 (92.6)**	**49851.2**
(a) Bird Island				
1. TS ~ SST + SSTG + SSHA + Wind + BATHY + EKE + d2col + (lon,lat)	Gaussian (untransformed)	Identity	-13905.1 (75.2)	27960.5
2. TS ~ SST + SSTG + SSHA + Wind + BATHY + EKE + d2col + (lon,lat)	Gaussian (log-transformed)	Identity	-13720.5 (76.4)	27593.9
3. **TS ~ SST + SSTG + SSHA + Wind + BATHY + EKE + d2col + (lon,lat)**	**Gamma**	**Log**	**-13702.8 (78.8)**	**27563.4**
(c) Cape Shirreff				
1. TS ~ SST + SSHA + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)	Gaussian (untransformed)	Identity	-27958.5 (80.5)	56077.9
2. TS ~ SST + SSHA + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)	Gaussian (log-transformed)	Identity	-27253.2 (86.6)	54679.6
3. **TS ~ SST + SSHA + SSHV + Wind + CHLa + EKE + d2col + (lon,lat)**	**Gamma**	**Log**	**-27232.9 (85.8)**	**54637.4**

LL, log-likelihood (degrees of freedom); AIC, Akaike's Information Criterion.

Chapter 5

Managing for change: Using vertebrate at sea habitat use to direct management efforts

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Abstract

To accurately understand and predict the current and future distributions of animals under a changing climate it is essential to establish historical ranges as baselines against which distribution shifts can be assessed. Management approaches also require comprehension of temporal variability in spatial distributions and habitat use that can occur over shorter time scales, such as inter-annually or seasonally. Focussing on the Southern Ocean, one of the most rapidly changing environments on Earth, we used Species Distribution Models (SDMs) and remotely sensed environmental data to reconstruct the likely historical foraging habitats of Antarctic fur seals (*Arctocephalus gazella*) from three populations during the non-breeding winter (Marion Island, Bird Island and Cape Shirreff), to assess whether habitat quality has changed in recent decades. We also quantified temporal variability in distributions to facilitate an assessment of the degree of overlap with fur seal habitat and Southern Ocean management areas (CCAMLR – Commission for the Conservation of Antarctic Marine Living Resources) and the potential for competition with fisheries during the non-breeding season. Despite notable changes to the physical ocean environment (sea surface temperature, wind speed and sea ice concentration in particular), the quality of Antarctic fur seal foraging habitat during the non-breeding season has remained relatively consistent over 20 years at Marion and Bird Islands, but less so at Cape Shirreff, where a reduction in sea ice cover has improved habitat accessibility. Spatio-temporally explicit SDMs identified variability in important habitats across the non-breeding winter. Some of these areas overlapped significantly with fisheries activities, suggesting a potential for competition with Southern Ocean fisheries for prey resources at several key periods throughout the winter. Substantial core habitat fell outside of the CCAMLR Convention Area, indicating that the

potential impacts of fisheries and climate change can occur remote from areas of active monitoring and management. Although CCAMLR has a precautionary and ecosystem based approach to fisheries management in the Southern Ocean, any changes to the physical environment or fisheries have the potential to affect how dependant species, such as Antarctic fur seals, are impacted.

Introduction

Recent changes to the Earth's climate are unequivocal and are effecting a wide range of species and communities from the equator to the poles in both terrestrial and marine ecosystems (Parmesan 2006). Polar regions are experiencing some of the strongest and fastest large-scale physical changes anywhere on Earth, with rapid rises in atmospheric and oceanic temperatures (Meredith & King 2005; Chapman & Walsh 2007) and accelerating loss of ice sheet mass (Pritchard *et al.* 2012). In the Southern Ocean, there is increasing evidence of the impacts of such changes on biological systems at various trophic levels (e.g. McMahon & Burton 2005; Montes-Hugo *et al.* 2009; Flores *et al.* 2012; Ropert-Coudert *et al.* 2015). Despite this, the links between physical changes and biological productivity remain poorly understood. However, any biological effects will be reflected in the responses of higher-trophic level species (seals, seabirds and whales) because they integrate and amplify the effects occurring at lower trophic levels (Hindell *et al.* 2003; Costa *et al.* 2010), often making them useful indicators of wider ecosystem change.

Changes in distribution is one potential response to climate change (Walther *et al.* 2002; Mueter & Litzow 2008) as species are forced towards higher latitudes or altitudes. Recently, studies into the distribution of highly mobile marine predators have focussed on predicting species responses to future climate change (e.g. Péron *et al.* 2012; Hazen *et al.* 2013; Spencer *et al.* 2016). However, to properly understand current and future distributions it is essential to establish historical distributions as baselines against which changes can be assessed (Lotze & Worm 2009). Historical records are often brief or fragmented (Swetnam *et al.* 1999) and biased towards terrestrial ecosystems (Elith & Leathwick 2009). For marine environments, historical distributions are mostly available for species of commercial interest (Bellier *et al.*

2007; Nye *et al.* 2009) and typically do not exist for remote regions such as the Southern Ocean. Conversely, baseline environmental data from remotely sensed sources (satellite) have been available since the 1980's, before the widespread use of animal-tracking devices to observe habitat use and at-sea distributions. Environmental data can be used to construct habitat models or Species Distribution Models (SDMs), which correlate species occurrence with environmental variables to explain or predict a species' distribution (Robinson *et al.* 2011). The inclusion of historical environmental data has the potential to hindcast SDMs to the likely historical distribution of top predators (Louzao *et al.* 2013), providing a baseline to assess future change and inform and appraise management decisions.

As well as potential changes over decadal time scales, the spatial distribution of many pelagic predators can be highly variable over shorter periods, such as inter-annually or seasonally (Forney & Barlow 1998; Pettex *et al.* 2012). This temporal variability is a major source of uncertainty in marine resource management and the effectiveness of SDMs as a management tool is determined in part by their ability to capture year-round habitat conditions (Becker *et al.* 2014). For species known to have pronounced seasonality in distribution, as is the case for many Southern Ocean predators (Cockell *et al.* 1999), SDMs that are spatio-temporally explicit at scales relevant to species movements and management objectives, will likely prove more informative. Although SDMs are under-utilised in marine species (Robinson *et al.* 2011) they have been effectively employed to inform habitat conservation, understand fisheries interactions and investigate the impacts of climate change in pelagic predators (See Robinson *et al.* 2011). Yet often, many do not consider the temporal shifts in habitat use and spatial distribution that can occur in wide-ranging animals.

In highly variable environments such as the Southern Ocean, significant environmental changes including the growth and decay of sea ice and fluctuations in primary productivity can occur on relatively short time scales of weeks to months (Gordon 1981; Clarke 1988). Such rapid environmental change can alter prey availability and the distribution of foraging predators (Cockell *et al.* 1999). Therefore, incorporation of temporal variability into SDMs for Southern Ocean predators is important for a variety of management approaches such as the design of marine protected areas, quantification of potential fisheries interactions and development of accurate ecosystem models.

Within this context, we studied the winter distribution of female Antarctic fur seals (*Arctocephalus gazella*, Peters, 1875), a highly mobile pelagic predator, from three Southern Ocean populations. By expanding SDMs previously established for each population (Arthur *et al.* In press) this study aims to: (1) Establish likely historical fur seal foraging habitat as a baseline to assess whether habitat quality has changed over recent decades, (2) describe temporal variability in foraging habitats across the non-breeding period and (3) assess the degree of spatio-temporal overlap with Southern Ocean management areas and the potential for interaction with fisheries during winter.

Methods

TRACKING INSTRUMENTATION AND ANALYSIS

Female Antarctic fur seals were tracked during their non-breeding winter migrations (April-December) at three colonies: Marion Island (Prince Edward Islands, 2008-13), Bird Island (South Georgia, 2008-11) and Cape Shirreff (South Shetland Islands, 2008-10) (Fig. 5.1a). Seals were equipped with a global-location sensing logger (GLS; British Antarctic Survey, Cambridge UK, 2.5-3.6 g) towards the end of lactation that was recovered when animals returned to pup the following season (n=184). Animal handling, device attachment and calibration procedures followed those outlined in Arthur *et al.* (2015). Non-breeding winter foraging trips encompassed the female's first post-weaning excursion until return to the colony in December. Individual foraging trips were identified and analysed separately (n=320). Location estimates were produced from the raw light and temperature data using the Bayesian approach of Sumner *et al.* (2009) in the R software (R Core Team 2014) package 'tripEstimation' (Sumner & Wotherspoon 2010) following the approach of Lea *et al.* (In review) detailed in full in Arthur *et al.* (2016, Supporting Information). Unprocessed GLS data are housed at Australian Antarctic Data Centre (http://data.aad.gov.au) for each colony: Marion Island (Lea *et al.* 2014a), Cape Shirreff (Lea *et al.* 2014b) and Bird Island (Lea *et al.* 2014c).

SPECIES DISTRIBUTION MODELS

Arthur *et al.* (In press) built SDMs for each colony to explain the relationship between the environment and the spatial distribution of Antarctic fur seal habitat during the non-breeding winter period. Briefly, the time spent per trip (hours) in each cell of a 0.6° x 0.6° raster grid (60 km x 60 km) covering the spatial extent of locations over all years (hereafter referred to as *time spent*) was modelled using winter climatologies of biologically relevant environmental predictor variables in a generalized additive modelling (GAM) framework. Environmental variables retained in final models included both static; bathymetry (BATHY) and distance to colony (d2col) and dynamic parameters; sea surface height anomaly (SSHa), variability of sea surface height anomaly (SSHV), sea surface temperature (SST), gradient of sea surface temperature (SSTG), chlorophyll a concentration (CHLa), wind speed (WIND) and eddy kinetic energy (EKE). Models were fit to a Gamma error structure with a log-link function and included a spatial autocorrelation term (Wood 2006). The best models for each colony are shown in Table 5.1a. Model predictions interpolated across the entire spatial domain of locations for each colony revealed the likely habitat use of Antarctic fur seals during winter for the years of study. We then defined core foraging areas as those within the 75% distribution quantile (see Arthur *et al.* In press, for full details).

Table 5.1. Summary of generalised additive models (GAMs) of the relationship between foraging effort (time spent per grid cell) and environmental variables for: (a) global colony models (from Arthur et al.) and (b) period models. TS = time spent, SSTG = sea surface temperature gradient, SSHA = sea surface height anomaly, SSHV = sea surface height variance, WIND = wind speed, CHLa = chlorophyll a concentration, BATHY = bathymetry, d2col = distance to colony, (lon,lat) = spatial autocorrelation term, period = period term.

Colony	Model formula	*k*	% dev	r^2	RMSE
	(a) Fitted habitat models				
Marion Island	TS ~ SST + SSHA + SSHV + WIND + CHLa + BATHY + EKE + d2col + (lon,lat)	10	73.3	0.704	14.3
Bird Island	TS ~ SST + SSTG + SSHA + WIND + BATHY + EKE + d2col + (lon,lat)	9	85.3	0.828	13.2
Cape Shirreff	TS ~ SST + SSHA + SSHV + WIND + CHLa + EKE + d2col + (lon,lat)	9	72.5	0.701	15.6
	(b) Period habitat models				
Marion Island	TS ~ SST, by=period + SSHA, by=period + SSHV, by=period + WIND, by=period + CHLa, by=period + BATHY, by=period + EKE, by=period + d2col, by=period + (lon,lat)	10	65.4	0.653	17.7
Bird Island	TS ~ SST, by=period + SSTG, by=period + SSHA, by=period + WIND, by=period + BATHY, by=period + EKE, by=period + d2col, by=period + (lon,lat)	9	57.5	0.430	30.3
Cape Shirreff	TS ~ SST, by=period + SSHA, by=period + SSHV, by=period + WIND, by=period + CHLa, by=period + EKE, by=period + d2col, by=period + (lon,lat)	9	53.1	0.525	22.9

k, number of parameters; % dev, per cent deviance explained by model, RMSE, root mean-squared error (in hours) obtained through k-fold cross validation.

PAST CHANGE AND RETROSPECTIVE HABITAT MODELLING

To assess whether the environmental characteristics of core foraging habitats have changed in the past three decades, we extracted all available winter environmental data for those variables retained in the final SDMs (Table A1) across the combined spatial extent of the three colonies for all years of study. We also included sea ice concentration (ICE) as although this parameter was not used in initial habitat modelling to describe fur seal habitat, large-scale changes to sea ice impacting top predators have occurred in the Southern Ocean in recent decades (e.g. Ropert-Coudert *et al.* 2015). Environmental data from the Australian Antarctic Data Centre were extracted using the R package 'raadtools' (Sumner 2015) and aggregated and re-projected to match the 0.6^o x 0.6^o grid used in the SDMs. For each dynamic variable we calculated the regression coefficient in each pixel across the temporal range of data (Table A1). This quantified the rate of change of each variable as a function of time, permitting an assessment of the long-term environmental trends. This also facilitated a direct comparison of the rate of change across variables measured on considerably different scales, for example a direct comparison could be made between SST measured in ^oC and WIND measured in m/s^{-2}.

To determine the historical foraging habitats of fur seals we mapped the spatial distribution of animals from the three colonies for the past 20 years across the observed spatial extent of tracking data. Dynamic variables were extracted as above for the period 1993-2013, spanning the earliest observations for all parameters used in the models (Table A1). CHLa data was not available prior to 1997, so this parameter was excluded. Static variables were extracted once. Data were then averaged to produce a mean parameter value per pixel for the five-yearly periods 1993-97, 1998-2002, 2003-07 and 2008-current observations. We then applied the SDM for each colony to these data to retrospectively predict historical foraging habitats that could be compared to current observations (2008 onwards).

The mean predicted *time spent* and standard error (SE) for each grid cell was used as a measure of quality and stability in predicted habitat during winter. The mean predicted *time spent* summarises the average foraging habitat while the SE represents the variability in foraging habitat during each period. Adapting the approaches of Louzao *et al.* (2013) and Bellier *et al.* (2007) to our study, habitat was classified into three categories: (1) *Regular foraging habitat* was defined as grid cells where the five-yearly mean and SE was higher than the overall mean, and lower than the overall SE, across all grid cells and 20 years. Seals consistently use these areas every year. (2) *Unfavourable foraging habitat* was defined as grid cells where the five-yearly mean and SE was lower than the overall mean, and lower than the overall SE, across all grid cells and 20 years. Seals rarely use these areas. (3) *Variable foraging habitat* encompassed remaining cells, which had a greater SE than the average across all grid cells and 20 years. Seals use these areas in some, but not all, years.

TEMPORAL VARIABILITY IN WINTER HABITAT USE AND OVERLAP WITH MANAGEMENT AREAS

The availability and use of foraging habitat by Antarctic fur seals is affected by intrinsic factors such as breeding status and extrinsic factors such sea ice cover, both of which contribute to seasonal variation in habitat use across the nine month winter period (Arthur *et al.* In press). Following the modelling approach outlined in Arthur *et al.* (In press), we developed SDMs for each of the three fur seal colonies in this study during three periods: early winter (March-May), mid winter (June-August) and late winter (September-December). Environmental data were subset by period and climatologies (mean value per cell for that period) were calculated for each parameter. The SDM for each colony was then applied to these data with the inclusion of a 'period' term (Table 5.1b).

In the Southern Ocean, the major fisheries management body is the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which manages the area south of the Antarctic Convergence. The CCAMLR Convention Area is divided into statistical areas (Statistical Area 48: Southern Atlantic, Statistical Area 58: Southern Indian, Statistical Area 88: Southern Pacific), which are further divided into subareas and divisions based on general oceanographic conditions and biological characteristics such as discrete populations of certain species (CCAMLR 2015b) (see Fig. 5.1a). We overlaid the predictions of foraging habitat for Antarctic fur seals from Marion Island, Bird Island and Cape Shirreff with CCAMLR management areas to determine regions of overlap during the three winter periods. Using data reported to CCAMLR by all fisheries operating inside the Convention Area (CCAMLR 2015a) we calculated the total fishing effort, and therefore potential for fisheries competition and interaction with fur seals, at these times. Fishing effort was expressed in fishing days (CCAMLR 2015a), representing the total number of days during which fishing occurred for all fisheries during fur seal tracking observations (2008-13 winters).

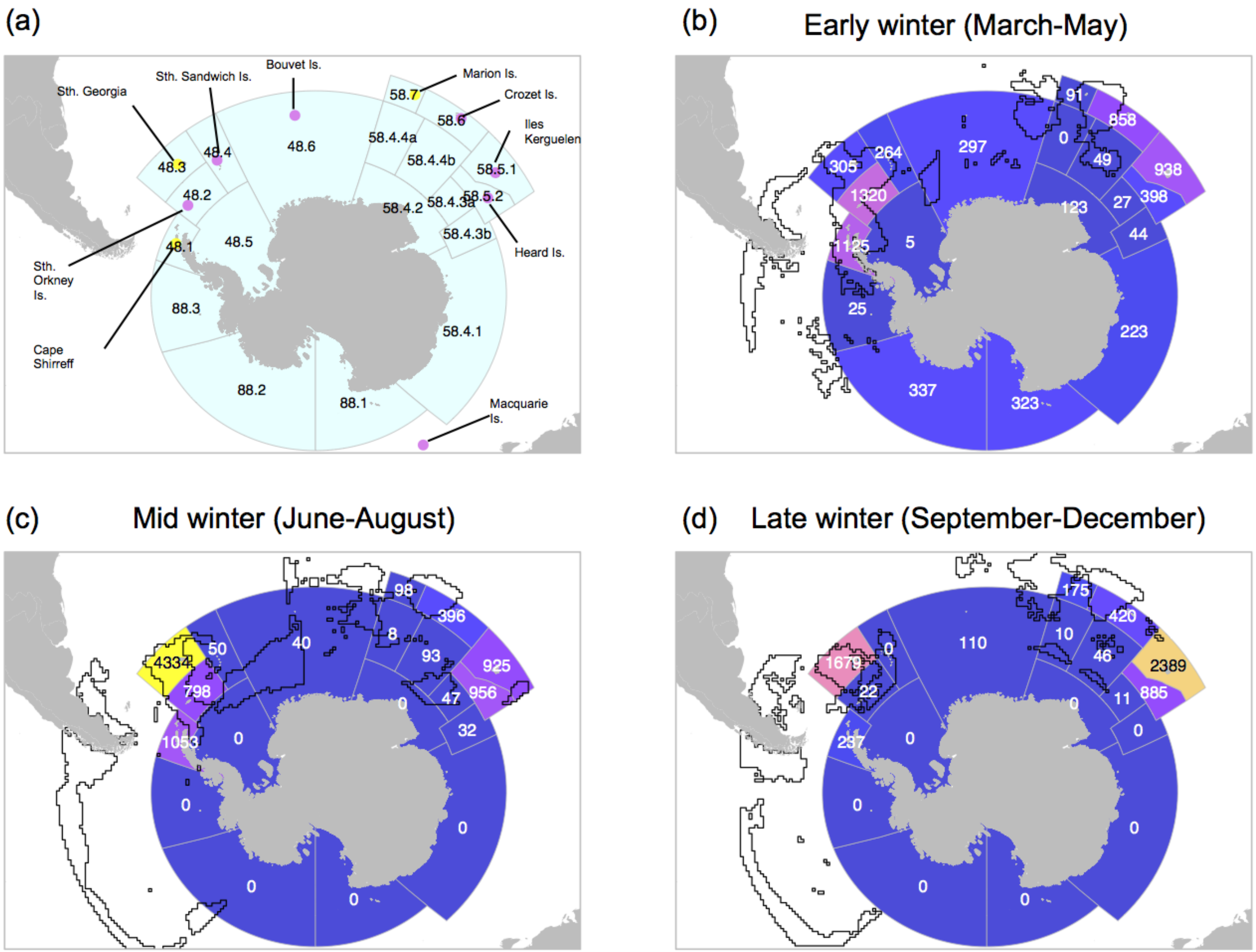


Figure 5.1. (a) Location of Antarctic fur seal breeding colonies. Study colonies are represented by yellow circles while all other colonies are represented by pink circles. The CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Convention Area is shown in light blue. Numbers represent the names of subareas and divisions comprising the Convention Area. **(b-d) Seasonal Antarctic fur seal habitat in relation to the CCAMLR Convention Area and fishing effort for (b) early, (c) mid and (d) late winter.** Core habitat for the Marion Island, Bird Island and Cape Shirreff colonies combined is represented by black lines. CCAMLR subareas and divisions are coloured by fishing effort (total number of winter fishing days 2008-13) with values overlaid.

Results

ENVIRONMENTAL CHANGE AND RETROSPECTIVE HABITAT MODELLING

There were clear long-term trends in several environmental parameters across the spatial domain of our study over recent decades, most notably SST, WIND and ICE (Fig. 5.2, Fig A1). Around Marion Island, there was an overall warming trend of SST (coefficients >0.2) and decrease in WIND (coefficients <-0.2) across contemporary core fur seal habitats, while ICE showed an increasing trend in the southern core habitats. Sea surface temperature also had a warming trend in contemporary core areas around Bird Island and the Patagonian Shelf as well as around the Western Antarctic Peninsula and oceanic foraging habitats to the far west of the study area. There was a cooling trend in contemporary core habitat off the south west coast of Chile and in southern regions of the Southern Atlantic Ocean. Generally, WIND showed a strong positive trend (coefficients >0.3) in some core seal habitats for Bird Island and Cape Shirreff, with the exception of waters off the Western Antarctic Peninsula, which had a negative trend. Sea ice concentration decreased in the core habitats around South Georgia and the Western Antarctic Peninsula (coefficients <-0.3).

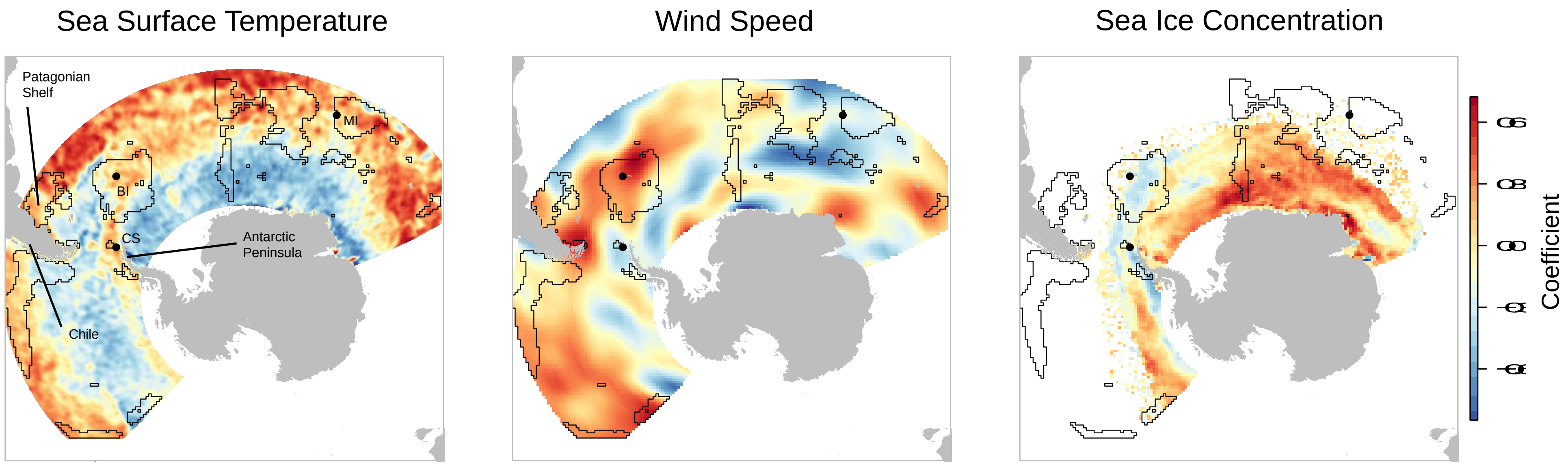


Figure 5.2. Regression coefficients for each pixel of a 0.6° x 0.6° grid matching the spatial extent of core Antarctic fur seal habitat (black lines) for sea surface temperature (SST, 1982-2013), wind magnitude (WIND, 1979-2013) and sea ice cover (ICE, 1979-2013). Locations of the Marion Island (MI), Bird Island (BI) and Cape Shirreff (CS) colonies are shown by black circles. The source of environmental data is provided in Table A1.

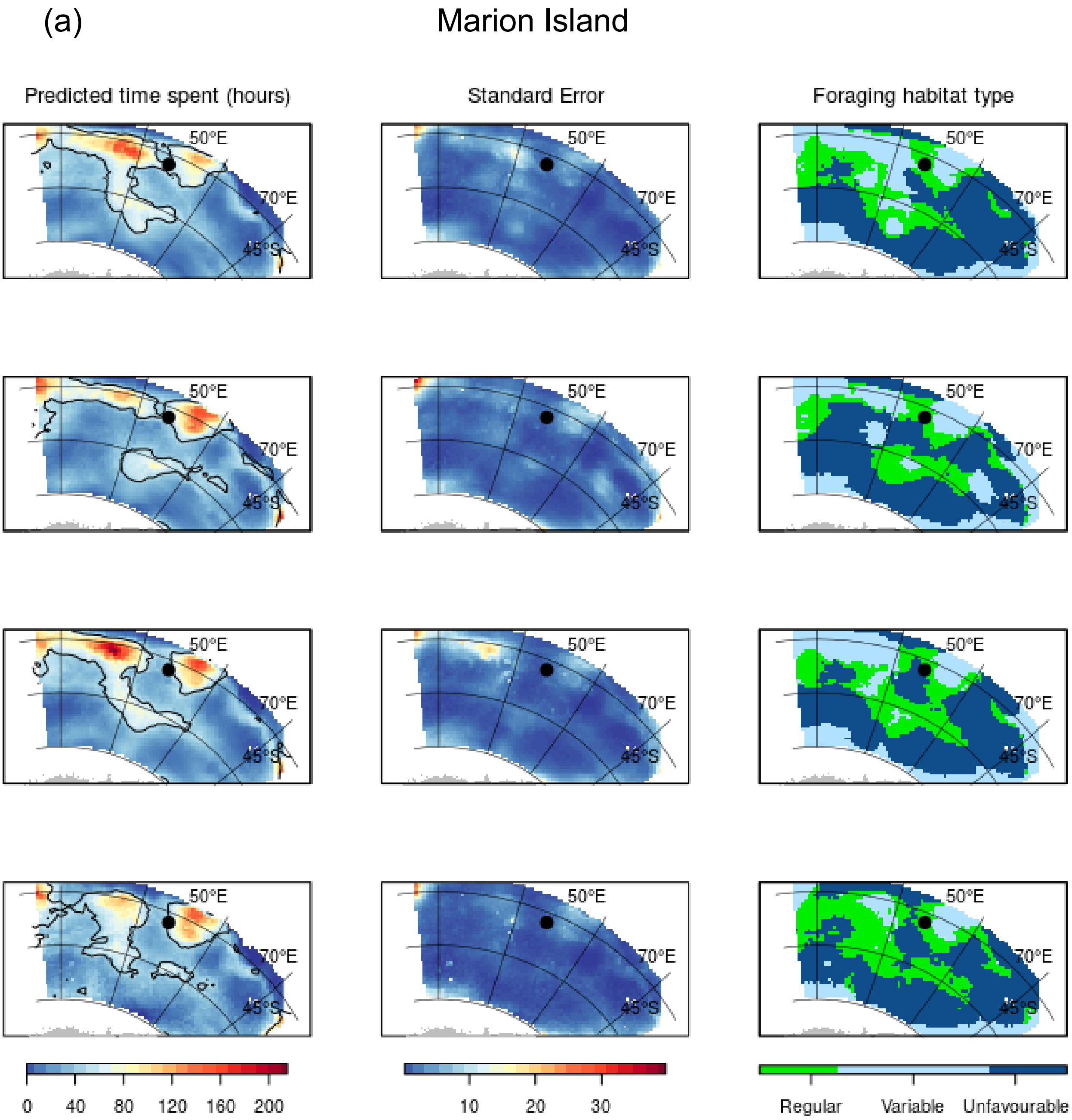
The SDMs for each colony were used to hindcast foraging habitat from 1993 to 2007, immediately before current observations commenced. At Marion Island, the hindcast *time spent* indicated little change in the location of core habitat and was consistently in close proximity to the east of the colony, as well as areas further to the west and south, matching 2008-13 observations (Fig. 5.3a). The SE of predictions was low across the spatial domain excepting the far northwest corner. Regular and unfavourable habitat increased by, on average, 4.1% (SD: ± 7.7) and 1.8% (SD: ± 4.4) each 5-years between 1993-2013. However, these increases were likely a product of a change in variable foraging habitat, which decreased by an average of 6.0% (SD: ± 11.1) over the same period as there was no consistent overall change to either regular or unfavourable habitat (Table 5.2).

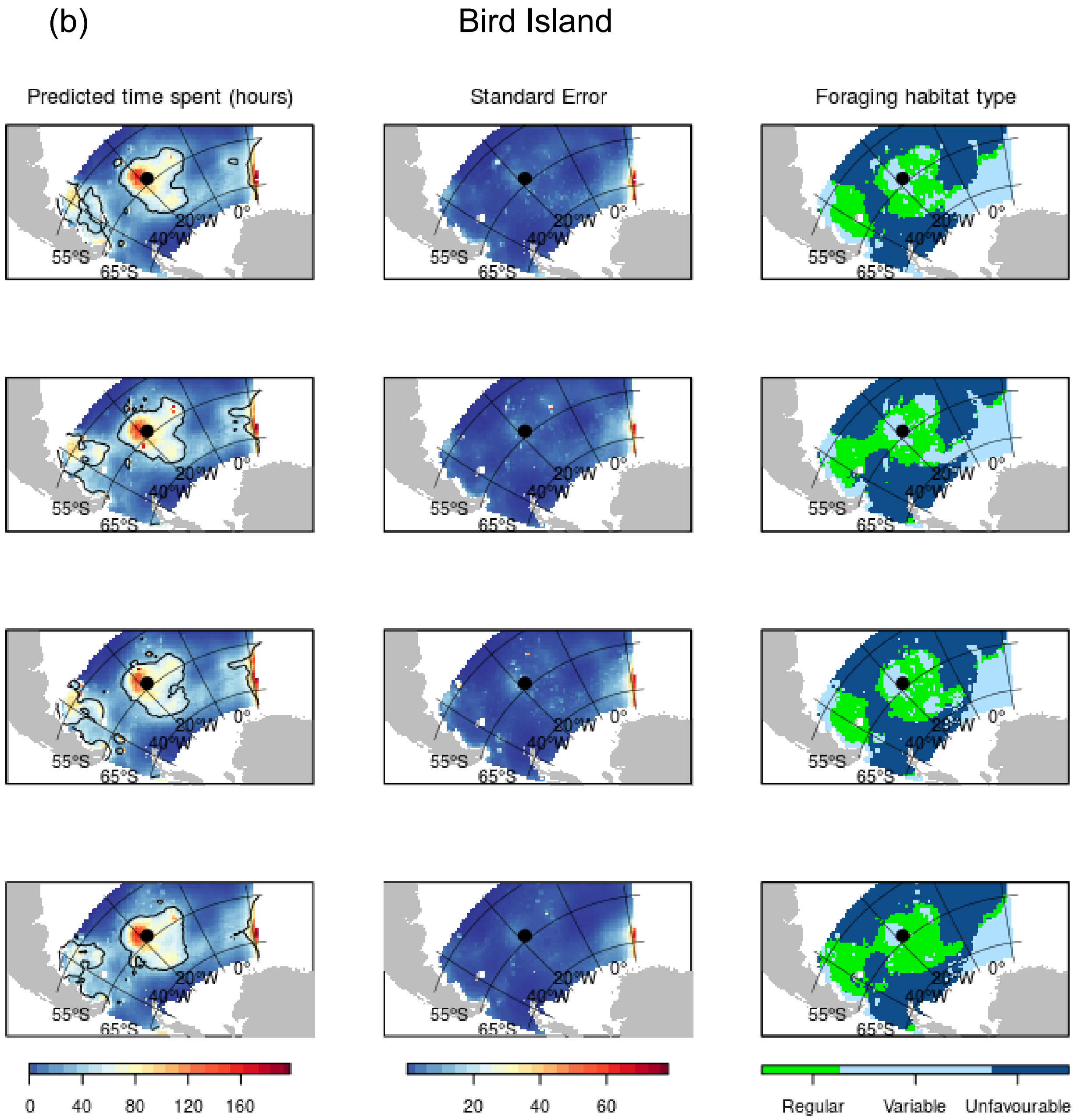
At Bird Island, the distribution of predicted *time spent* for five-yearly periods between 1993-2007 was consistent and closely matched 2008-11 observations (Fig. 5.3b). Core foraging habitat for this entire period included waters around South Gerogia and the Patagonian Shelf. Core habitat was also identified for each period at the extreme east of the population's range, however the high associated SE suggests these predictions are not robust. The broad distribution of regular foraging habitat was consistent between 1993-2011 (Fig. 5.3b), with regular and unfavourable habitat changing by, on average, 3.1% (SD: ± 5.6) and 1.1% (SD: ± 1.3) per five years. Variable habitat displayed a constant decrease across the 20 years (Table 5.2).

Hindcasted *time spent* values at Capre Shirreff between 1993-2008 also revealed core foraging areas were broadly consistent across each five-year period and closely matched the observations from 2008-10 (Fig. 5.3c). Core areas included waters off the southwest of Chile extending west, the Patagonian shelf and waters around South Georgia. The SE of predictions was low across the spatial domain except for in the far southeast in the northern Weddell Sea. The distribution of regular foraging habitat around the Western Antarctic Peninsula and South Georgia shifted between 1993-2010. Overall, regular foraging habitat increased by 4.6% (SD: ± 5.3) every five years, while variable habitat decreased by 4.6% (SD: ± 5.4).

Table 5.2. The number of cells (ncells) and percentage change (% change) in winter foraging habitat type between five-yearly periods from 1993 to current observations (2013 Marion Island, 2011 Bird Island, 2010 Cape Shirreff). Regular habitat = grid cells where the five-yearly mean and SE was higher than the overall mean, and lower than the overall SE, across all grid cells and 20 years, Unfavourable habitat = grid cells where the five-yearly mean and SE was lower than the overall mean, and lower than the overall SE, across all grid cells and 20 years, Variable habitat = grid cells which had a greater SE than the average across all grid cells and 20 years.

Colony	Time period	Regular habitat		Unfavourable habitat		Variable habitat	
		ncells	% change	ncells	% change	ncells	% change
Marion Is.	1993-97	2034		2948		2229	
	1998-2002	1959	-3.7	2995	1.6	2257	1.2
	2003-07	2041	4.2	2920	-2.5	2250	-0.3
	2008-13	2281	11.8	3105	6.3	1825	-18.9
	Mean		**4.1 ± 7.7**		**1.8 ± 4.4**		**-6.0 ± 11.1**
Bird Is.	1993-97	2323		3245		2500	
	1998-2002	2271	-2.2	3288	1.3	2501	<0.0
	2003-07	2329	2.5	3279	-0.3	2452	-1.9
	2008-11	2541	9.0	3358	2.4	2217	-9.6
	Mean		**3.1 ± 5.6**		**1.1 ± 1.3**		**-3.8 ± 5.0**
Cape Shirreff	1993-97	1832		4338		2736	
	1998-2002	1993	8.8	4300	-0.8	2575	-5.9
	2003-07	1965	-1.4	4303	<0.0	2610	1.4
	2008-10	2093	6.5	4542	5.5	2365	-9.4
	Mean		**4.6 ± 5.3**		**1.5 ± 3.4**		**-4.6 ± 5.5**


(a)
Marion Island
Predicted time spent (hours)
Standard Error
Foraging habitat type
50°E
70°E
45°S
0
40
80
120
160
200
10
20
30
Regular
Variable
Unfavourable



(b)
Bird Island
Predicted time spent (hours)
Standard Error
Foraging habitat type
20°W
0°
40°W
55°S
65°S
0
40
80
120
160
20
40
60
Regular
Variable
Unfavourable

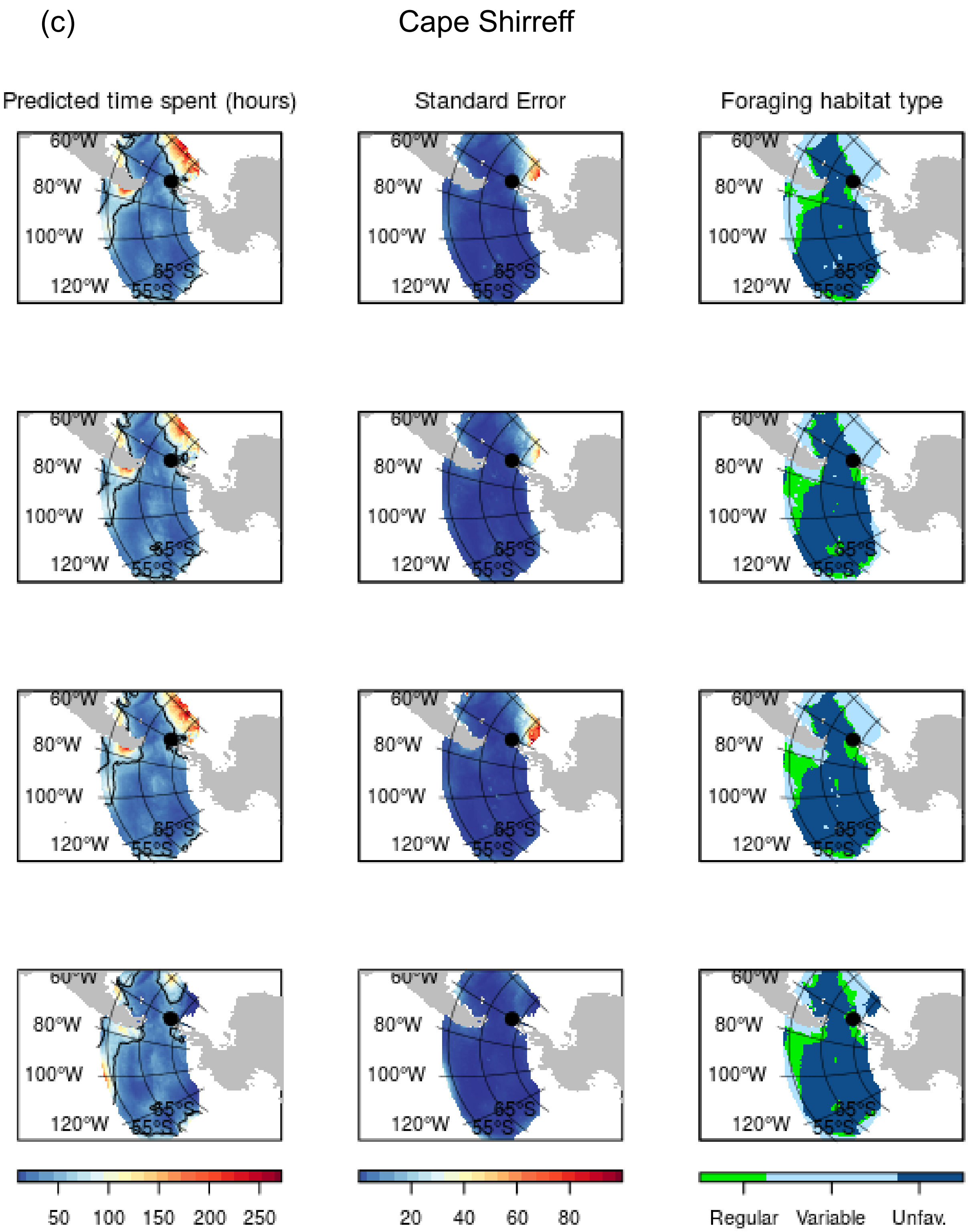


Figure 5.3. Mean predicted time spent (hours), standard error (SE) and habitat suitability (foraging habitat type) for five-yearly periods between 1993 to current observations for female Antarctic fur seals from (a) Marion Island, (b) Bird Island and (c) Cape Shirreff during the non-breeding winter. Core habitats (75% distribution areas) are shown in black lines. Black circles represent colony locations. Regular foraging habitat is observed annually (higher than 20 year average mean and low SE); variable foraging habitat is used by animals in some years (higher than 20 year average SE); Unfavourable foraging habitat is rarely used by animals (lower than 20 year average mean and SE).

TEMPORAL VARIABILITY IN WINTER HABITAT USE

To assess temporal variability of core seal habitat we split the non-breeding winter into three periods: early, mid and late. At Marion Island, the spatial distribution of observed *time spent* showed clear variations in both latitude and longitude across the winter (Fig. 5.4). Regions of relatively high use were located further south (south of 55°S) in early and mid winter than in late winter, following the expansion of sea ice (Fig. 5.4). Longitudinally distant areas, particularly to the far west of Marion Island (west of 20°E), were used more in mid and late winter. *Time spent* was consistently high to the east and west of the colony in relative close proximity throughout the winter. The Marion Island SDM with 'period' term had normally distributed model residuals and explained 65.4% of the deviance in the data. The model also had good predictive performance in cross-validation (r^2 = 0.653, RMSE = 17.71).

The spatial distribution of *time spent* for the Bird Island population was mostly concentrated in local waters around South Georgia and showed little temporal variability over the winter (Fig. 5.4). There were, however, seasonal differences in the use of the Patagonian Shelf and associated shelf break, with *time spent* in this area increasing across the winter. The residuals of the SDM with 'period' term were normally distributed and model assessment suggested a good fit to the observations, explaining 57.5% of the deviance and having reasonable cross-validation predictive ability (r^2 = 0.43, RMSE = 30.32).

At Cape Shirreff, there was clear temporal variability in *time spent* values across the winter (Fig. 5.4). In early winter, *time spent* was high close to the colony and south along the Western Antarctic Peninsula. Seals spent very little time in these areas as the winter progressed and sea ice formed (Fig. 5.4). Concurrently, *time spent* in waters off the southwest coast of Chile was low in early winter and increased in mid and late winter. Seals from Cape Shirreff also increased their longitudinal range further into the Southern Pacific Ocean throughout winter. The SDM with 'period' term had normally distributed residuals and explained 53.1% of the deviance in the data. The model had good predictive performance (r^2 = 0.525, RMSE = 22.9).

The models for each colony were interpolated across the spatial domain for each period of the winter. The predicted core habitat for all three colonies combined is presented in Fig. 5.1b-d.

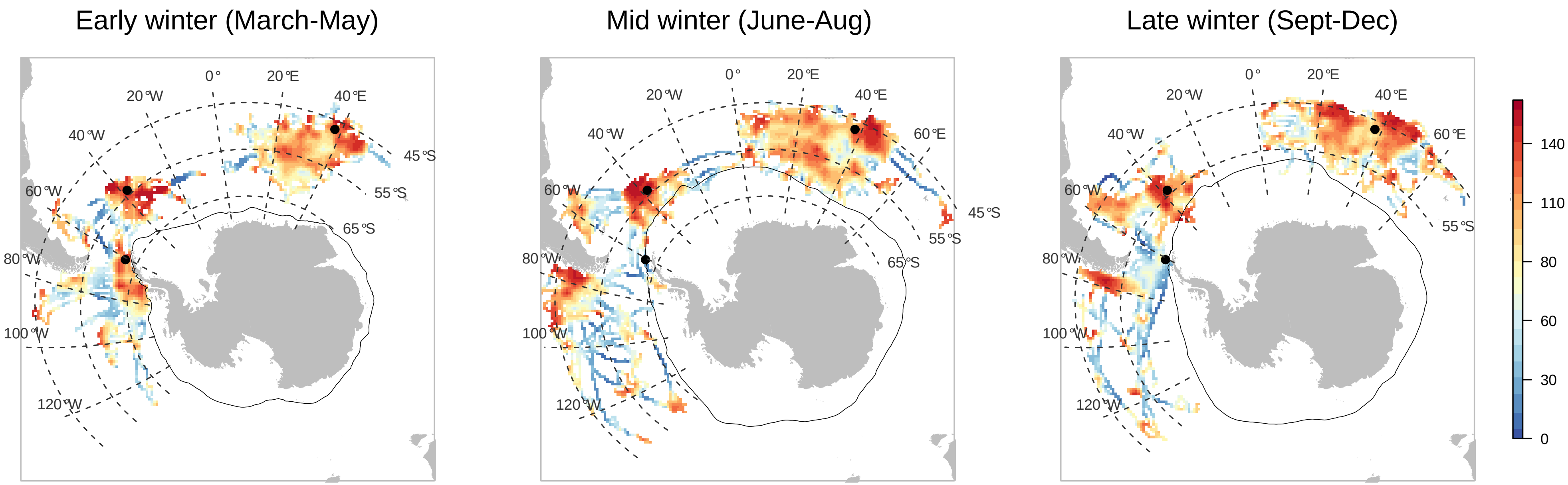


Figure 5.4. Observed habitat use (time spent in hours per cell of a 0.6º x 0.6º grid) for 184 female Antarctic fur seals from Marion Island (2008-2013), Bird Island (2008-2011) and Cape Shirreff (2008-2010) (black circles) across three non-breeding periods: early (March-May), mid (June-August) and late (September-December). The average position of the sea ice edge for each period is shown by black lines.

OVERLAP WITH MANAGEMENT AREAS AND FISHING EFFORT

In early winter fur seal habitat overlapped significantly with CCAMLR subareas 88.3 and 48.1 along the Western Antarctic Peninsula, and subareas 48.2 and 48.3 around the South Orkney Islands and South Georgia respectively (Fig. 5.1b). Significant overlap was also observed in subarea 48.6 and divisions 58.7 and 58.6 around Marion and Crozet Islands respectively, and 58.4.4b south of Crozet Islands. In mid winter (Fig. 5.1c), core fur seal habitat in the South Atlantic sector was congruent with subareas 48.2 and 48.3. Substantial core habitat overlapped with subarea 48.6. In the Southern Indian sector, mid winter habitat was observed in divisions 58.7 and 58.6, and 58.5.1 and 58.5.2 around Iles Kerguelen and Heard Island. Significant overlap also occurred with divisions 58.4.4b and 58.4.3a south west of Kerguelen Island. In late winter (Fig. 5.1d), core habitat overlapped with subareas 48.2, 48.3 and 48.4 (around the South Sandwich Islands) in the Southern Atlantic sector. In the Southern Indian sector, core foraging habitat in late winter overlapped with division 58.6 and south to divisions 58.4.4a and 58.4.4b. During all three seasons substantial areas of core habitat occurred outside of the CCAMLR convention area, notably the Patagonian Shelf, the southern coast of Chile and pelagic waters extending west, and areas to the west of Marion Island.

The fishing effort in CCAMLR areas of significant spatio-temporal overlap with core seal habitat is presented in Fig. 5.1 and Table 5.3. In early winter (Fig. 5.1b), high fishing effort occurred in subareas 48.2 around the South Orkney Islands and 48.1 along the Western Antarctic Peninsula, at 1320 and 1125 fishing days respectively (Table 5.3). Fishing effort was also high, 858 days, in division 58.6 around the Crozet Islands. Fishing effort during mid winter (Fig. 5.1c) congruent to seal habitat was particularly high in subarea 48.3 around South Georgia at 4334 fishing days, and was also high in subarea 48.2 (798 days, Table 5.3). In the Southern Indian sector, high mid winter fishing effort overlapped with seal habitat in subarea 58.5.1 (925 days) east of Iles Kerguelen (Table 5.3). During late winter (Fig. 5.1d), core fur seal habitat was congruent with high fishing effort in subareas 48.3 (1679 days) and division 58.6 (420 days, Table 5.3).

Table 5.3. The winter fishing effort of all fisheries operating in the CCAMLR Convention Area. Fishing effort is expressed as total fishing days during the winters of 2008-13 inclusive for each of the 19 CCAMLR subareas/divisions. Early winter = March-May, Mid winter = June-August, Late winter = September-December, Use by AFS = subareas/divisions that incorporated core Antarctic fur seal habitat at some period during winter.

Subarea/Division	Fishing effort			Use by AFS
	Early winter	Mid winter	Late winter	
Southern Atlantic (Area 48)				
48.1	1125	1053	237	early, mid
48.2	1320	798	22	early, mid, late
48.3	305	4334	1679	early, mid, late
48.4	264	50	0	early, mid, late
48.5	5	0	0	early, mid
48.6	297	40	110	early, mid, late
Southern Indian (Area 58)				
58.4.1	223	0	0	-
58.4.2	123	0	0	mid
58.4.3a	27	47	11	mid, late
58.4.3b	44	32	0	-
58.4.4a	0	8	10	early, mid, late
58.4.4b	49	93	46	early, mid, late
58.5.1	938	925	2389	mid
58.5.2	398	956	885	mid
58.6	858	396	420	early, mid, late
58.7	91	98	175	early, mid, late
Southern Pacific (Area 88)				
88.1	323	0	0	-
88.2	337	0	0	early, mid
88.3	25	0	0	early, mid

Discussion

BASELINE FORAGING HABITATS OF ANTARCTIC FUR SEALS

By hindcasting pre-existing SDMs we have revealed the historical foraging habitats for three Antarctic fur seal populations in the Southern Ocean. This necessitated extrapolating in environmental space, which is inherently risky as, in this instance, there are no past observations to support predictions (Elith & Leathwick 2009). However, such extrapolation is necessary here and similar temporal transferability of SDMs has successfully being shown for albatross in the Southern Ocean (Louzao *et al.* 2013). There has been notable change over the last ~30 years to the winter physical ocean environment in the regions which today have relatively high time spent by female Antarctic fur seals. In particular, there were long term trends in SST, WIND and ICE during winter. The direction of trends varied regionally, signifying environmental change pressures are colony specific. In the Southern Indian sector, habitats used by Marion Island animals have undergone warming of surface waters and an overall weakening in wind speeds, while southern habitats have shown an increasing trend in sea ice concentration. Foraging habitats of the Bird Island and Cape Shirreff populations in the Southern Atlantic sector have experienced an overall increase in wind speeds and a loss of sea ice concentration. Changes to SST varied, with some habitats warming while others have cooled. These observations are in broad agreement with more comprehensive studies of the wider Southern Ocean climate system (For a review see Mayewski *et al.* 2009).

It remains poorly understood how the biological component of Southern Ocean ecosystems will be affected by climate change. However, several studies have shown links between the physical effects of climate change and biological responses.

For example, warming of waters and a shift towards positive phases of the Southern Annular Mode, the dominant mode of atmospheric variability in the Southern Ocean, is expected to lead to a deepening of the mixed layer depth and associated negative impacts for biological productivity (Sallée *et al.* 2010). Changes to water temperature and declines in sea ice are affecting the abundance, distribution and life cycle of prey species, such as Antarctic krill (Smetacek & Nicol 2005; Flores *et al.* 2012). Wind speed can also impact the distribution of prey (Pelland *et al.* 2014; Sterling *et al.* 2014), with stronger winds leading to increased turbulence and mixing which can drive prey deeper in the water column (Incze *et al.* 2001). Such changes could lead to an overall shift in the vertical distribution of prey, forcing seals to dive deeper.

Despite obvious environmental changes, the hindcasting of likely historical distributions of foraging habitats revealed these to be relatively stable since 1993, particularly at Marion and Bird Islands. The population of Antarctic fur seals at both Marion Island and South Georgia has grown rapidly since harvesting in the 18th and 19th centuries (Payne 1977; Hofmeyr *et al.* 2006), although population growth has slowed or plateaued in recent years (Boyd 1993; Wege *et al.* 2016). Such rapid population recovery was likely facilitated by favourable conditions, namely reduced competition for prey (Croxall *et al.* 1988), which in the case of the South Georgia population comprises the largest concentrations of krill in the Southern Ocean (Reid & Arnould 1996). However, we note that population growth has slowed in concert with environmental changes, particularly at South Georgia, suggesting that changes to the physical environment may, in part, be playing a role. Although this is difficult to disentangle from the population reaching carrying capacity, the carrying capacity of any population is not a fixed point and varies as the environment changes (Begon *et al.* 2006). At South Georgia, increases in ecosystem variability (driven by positive El

Nino Southern Oscillation anomalies) and lower krill availability during the breeding season since 1990, have increased the fitness costs associated with breeding for females and resulted in significant changes to population structure and phenotypic and genetic variation (Forcada *et al.* 2008; Forcada & Hoffman 2014). Population-level changes such as these may affect the use of winter foraging habitat by animals in the future.

At Cape Shirreff, hindcasting showed that foraging habitats may have changed in recent decades, with a persistent expansion of regular regions with high time spent between 1993 and 2010. Increases were clearest around the Western Antarctic Peninsula and the South Orkney Islands towards South Georgia. These regions of the Southern Ocean have experienced some of the strongest warming on Earth, with increases in both air and ocean temperatures (Vaughan *et al.* 2003; Meredith & King 2005) concomitant with a reduction in sea ice (Stammerjohn *et al.* 2008). Indeed our results can link improved foraging habitat quality for Cape Shirreff animals to areas that have experienced ocean warming and a reduction of winter sea ice. Antarctic sea ice can present a barrier to marine predators lacking suitable adaptations, excluding them from an area (Ainley *et al.* 2003). Unlike other Antarctic pinnipeds, Antarctic fur seals are not considered an ice obligate species and typically avoid areas of significant ice cover (see Fig 5.4). The reduction of winter sea ice on the Western Antarctic Peninsula and waters south of South Georgia has therefore allowed foraging animals to access this previously unfavourable habitat. Similar climate-driven improvements in Southern Ocean habitat quality have been reported for wandering albatross (*Diomedea exulans*), with changes to wind patterns (Weimerskirch *et al.* 2012) and southern elephant seals (*Mirounga leonina*), whose population at

Macquarie Island responds positively to reduced sea ice cover (van den Hoff *et al.* 2014).

The increase in habitat availability at Cape Shirreff is not reflected in recent population trends of the colony. Although the population has grown rapidly since re-colonisation in the late 1950's, pup production slowed towards carrying capacity by the early 2000's (Hucke-Gaete *et al.* 2004), with evidence of a population decline since (Schwarz *et al.* 2013). However, this is likely the result of top-down control by leopard seal (*Hydrurga leptonyx*) predation on pups, rather than bottom-up processes, and it is predicted that the population would increase in size if this pressure were removed (Schwarz *et al.* 2013). The expansion of winter foraging habitat reported here may, therefore, facilitate any potential expansion of this population.

TEMPORAL HABITAT USE AND IMPLICATIONS FOR MANAGEMENT

Spatio-temporally explicit SDMs were developed for the three Antarctic fur seal study populations which identified important habitat at several stages of the Southern Ocean winter, with core areas differing between early, mid and late winter, particularly at Marion Island and Cape Shirreff. Use of these habitats will ultimately be driven by prey availability and the temporal changes in diet reported for female Antarctic fur seals during winter (Walters 2014) reflect this. The distribution of fur seals during winter is also influenced by the extent of sea ice, with animals being excluded from more southerly areas with the expansion of winter sea ice (see Fig 5.4).

Appreciation of the changes in habitat use of marine animals throughout their annual cycle is necessary to inform a range of management measures such as the development of realistic ecosystem models, the design of marine protected areas and assessment of fisheries interactions. In the Southern Ocean, CCAMLR seeks to manage the ecological impacts of commercial harvests. A key component is monitoring the life-history parameters of select dependant predator species, one of which is the Antarctic fur seal, in the CCAMLR Ecosystem Monitoring Program (CEMP) (CCAMLR 2013a). The parameters measured in CEMP operate at various spatial and temporal scales (Kock *et al.* 2007) and may reflect changes in the ecosystem over days to months (Agnew 1997). Ultimately, demographic measures such as pup production in Antarctic fur seal is, in part, determined by environmental conditions and prey availability during the preceding winter/spring (Boyd *et al.* 1995). In order to effectively interpret the response of Antarctic fur seals in the CCAMLR context it is important to quantify habitat use and potential overlap with fisheries outside of the breeding season, when the majority of population monitoring currently occurs. The spatio-temporally explicit winter SDMs developed here are directly relevant to this management framework.

Female Antarctic fur seals from the three study populations foraged in 16 of the 19 CCAMLR subareas and divisions throughout the winter (Table 5.3). Core fur seal habitat coincided with high fishing effort in a number of these areas, suggesting there is a potential for operational interaction with fisheries. Although there has been incidental by-catch of Antarctic fur seals in CCAMLR managed fisheries (AFMA 2003; Hooper *et al.* 2005), all krill fishing nets are now fitted with a seal exclusion device and there have been no reports of seal by-catch since (CCAMLR 2015c). Therefore, competition is the most likely interaction that Antarctic fur seals will have with Southern Ocean fisheries.

Foraging habitat was relatively stable throughout the winter for Bird Island animals, with waters around South Georgia and the South Orkney Islands important habitat. Fishing effort was also consistently high in this area across the winter. Bottom-up forces have a substantial influence on the population of Antarctic fur seals at South Georgia, with the availability and predictability of a major prey source, Antarctic krill (*Euphausia superba*), a key factor (Reid & Croxall 2001). Indeed offspring production is strongly associated with krill size and abundance in a suite of predators from South Georgia including Antarctic fur seals, albatross and penguins (Croxall *et al.* 1999; Murphy *et al.* 2007). The Southern Ocean krill harvest is focussed around South Georgia, the South Orkney and South Shetland Islands in winter (see Croxall & Nicol 2004). The majority of female Antarctic fur seals from South Georgia in this study overlapped significantly with these areas of high fishing effort and did not migrate away from the krill fishery in winter, unlike other species (Trathan *et al.* 2012). Our results suggest a previously undocumented potential for competition with fisheries exists during winter, which further strengthens the importance of on going monitoring of the South Georgia fur seal population under CEMP.

In the Southern Indian Ocean, core foraging habitats of the Marion Island population coincided with periods of high fishing effort in several regions, most notably between Marion and Crozet Islands and extending south. The productivity of this area is used by foraging predators from Marion Island (de Bruyn *et al.* 2009; Arthur *et al.* In press). This region of the Southern Ocean is also the focus of finfish fisheries particularly for Patagonian toothfish (*Dissostichus eleginoides*), mackerel icefish (*Champsocephalus gunnari*) and grey rockcod (*Lepidonotothen squamifrons*) (CCAMLR 2013b), the latter two of which are potentially important prey in the diet of Antarctic fur seals in the Southern Indian Ocean (Lea *et al.* 2002a; Walters 2014). Fishing effort was particularly high in early winter (March-May). The potential for competition with Marion Island fur seals is greatest in this post-breeding period. Female Antarctic fur seals invest resources in lactation at a greater rate than other otariid seals and can incur high fitness costs (Forcada *et al.* 2008). Subareas 58.6 and 58.7 concurrent with high fishing effort are important for females targeting a reliable foraging habitat in close proximity to the colony in order to recover body condition after the breeding season (Arthur *et al.* In press). The current catch in these areas, however, consist mostly of Patagonian toothfish, which is not a species readily consumed by Antarctic fur seals. Although competition appears not to be an issue at present, any expansion of fisheries for other species into these areas warrants consideration of the importance of this habitat to fur seals at this time of year.

In late winter there is also the potential for competition with finfish fisheries east of Iles Kerguelen. The austral spring is an important period for females as it coincides with the increasing energetic demands of gestation after delayed implantation (Boyd 1996) and reproductive success in the coming summer can be linked to prey availability at this time of year (Boyd *et al.* 1995). It is, therefore, a critical time for the monitoring of potential fisheries competition. Although the use of this area by females from Marion Island appears minimal, the identification of this region as valuable foraging habitat by our models suggest that animals from geographically closer populations, such as Iles Kerguelen and Heard Island, where no non-breeding habitat information currently exist, may be more effected by any potential fisheries competition in this region. Our results are in broad agreement with Guinet *et al.* (2001), who used a similar probabilistic modelling approach and identified these areas as important foraging habitat for female Antarctic fur seals from Iles Kerguelen during the breeding season. Our findings extend this to suggest that areas east of Iles Kerguelen are also likely to be important habitat for animals from this population during the non-breeding season.

Although CCAMLR has a precautionary and ecosystem based approach to fisheries management, changes to the physical environment and developments in the fishing industry (such as the recent expansion of the krill fishery into more southern waters in winter due to a lack of sea ice, Nicol *et al.* 2012) have the potential to affect how dependant species, such as Antarctic fur seals, are impacted. The results of our study also show that substantial amounts of the foraging habitat of Antarctic fur seals falls outside the CCAMLR Convention Area at all stages of the non-breeding season. In particular the southern coast of Chile and associated pelagic waters extending west, the Patagonian Shelf and areas west of Marion Island were consistently important habitats throughout the winter. These areas have large active fisheries (UN Food and Agriculture Organization 1997), in some cases bigger than in the Southern Ocean, and are likely to be less well managed in regards to the impacts of commercial harvesting on predator populations compared with the ecosystem-based approach of CCAMLR. As animals from all three populations in this study consistently foraged outside the CCAMLR Convention Area during winter, it is worth noting that events or impacts occurring in these regions will be reflected in populations within the Convention Area, providing an important context for the interpretation of the CCAMLR Ecosystem Monitoring Program.

Acknowledgements

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Supporting Information

Appendix A

Table A1. The source and temporal range of environmental predictor variables used in habitat models. Data are from the Australian Antarctic Data Centre (http://data.aad.gov.au)

Variable	Source	Available temporal range
Sea surface temperature (SST)	OISST	1982-2013
Sea surface temperature gradient (SSTG)	OISST	1982-2013
Sea surface height anomaly (SSHA)	AVISO	1993-2013
Sea surface height anomaly variance (SSHV)	AVISO	1993-2013
Chlorophyll a concentration (CHLa)	SeaWiFS	1997-2013
Wind speed (WIND)	NCEP/DOE AMIP-II	1979-2013
Surface currents (CURR*u* and CURR*v*)	AVISO	1993-2013
Eddy kinetic energy (EKE)	Derived from u and v current components*	1993-2013
Sea ice concentration (ICE)	NSIDC	1979-2013
Bathymetry (BATHY)	gebco_08	static

*Eddy kinetic energy calculation: $EKE = ½ (\mathrm{CURR}u^2 + \mathrm{CURR}v^2)$

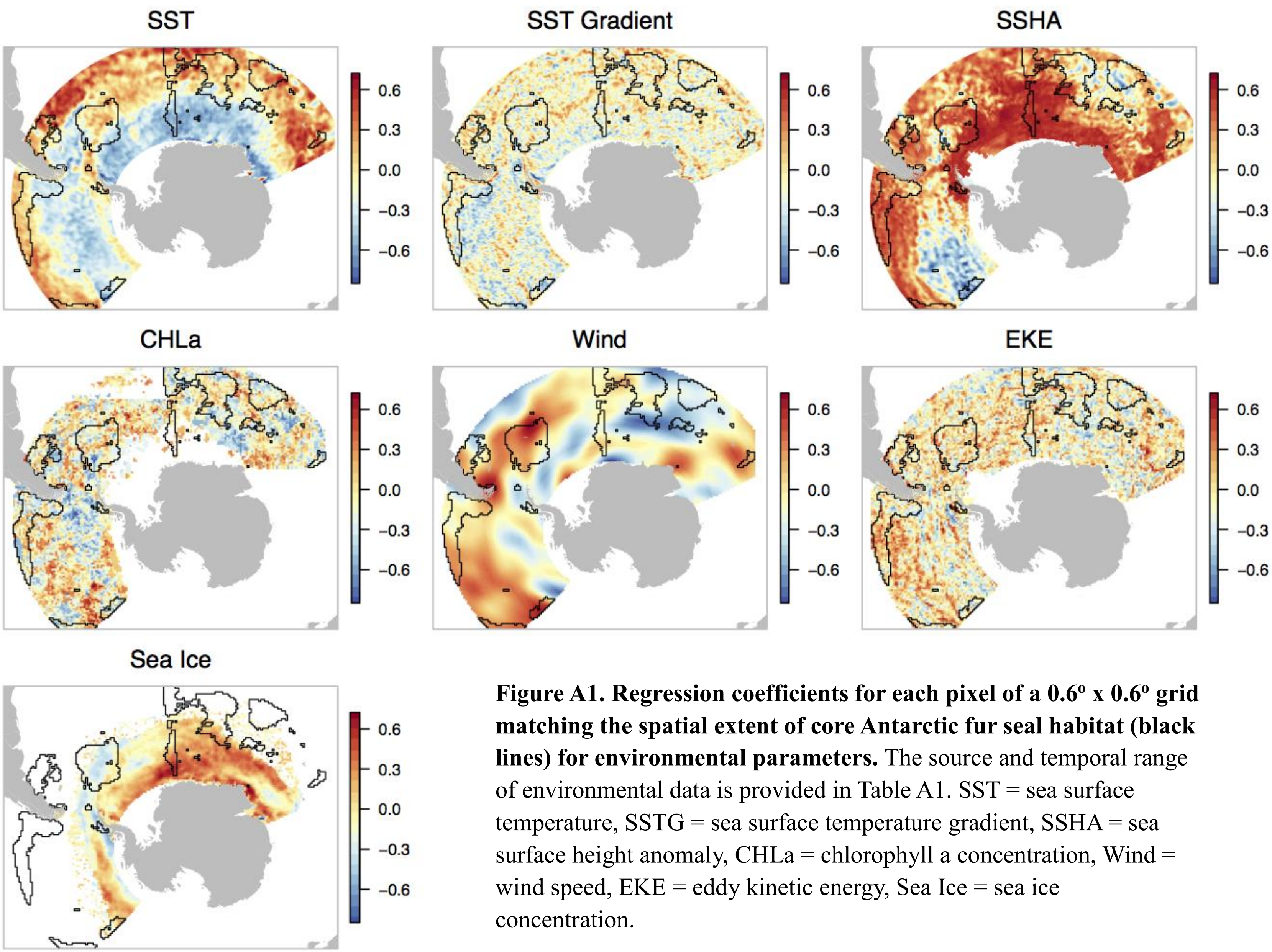

Figure A1. Regression coefficients for each pixel of a 0.6º x 0.6º grid matching the spatial extent of core Antarctic fur seal habitat (black lines) for environmental parameters. The source and temporal range of environmental data is provided in Table A1. SST = sea surface temperature, SSTG = sea surface temperature gradient, SSHA = sea surface height anomaly, CHLa = chlorophyll a concentration, Wind = wind speed, EKE = eddy kinetic energy, Sea Ice = sea ice concentration.

Chapter 6

General Discussion

This thesis aimed to quantify the non-breeding, winter habitat use and foraging ecology of Antarctic fur seals and provide new insights into how these are related to environmental conditions and management considerations in the Southern Ocean. Understanding the foraging movements of marine predators during the non-breeding season, when many species spend most of their time at sea and can roam over large areas, remains a major challenge in marine science. Using a suite of bio-logging and modelling approaches, this study has produced considerable new information on the ecology of this major Southern Ocean predator. This discussion will provide an overview and synthesis of the main findings in a broad ecological context, particularly with regard to the scales of habitat use and foraging ecology and implications for management.

Observing habitat use and foraging behaviour: the importance of scale

The consideration of scale is central in ecology, involving phenomena that occur on different scales of space, time and ecological organisation (Levin 1992). In animal movement studies, the spatial and temporal scales observed ultimately affect the biological information that can be quantified. For example, observations over days to weeks may cover movements from tens to hundreds of kilometres and provide insight into foraging trips, while observations during weeks to months may span hundreds to thousands of kilometres and reveal the strategies of individual animals, and movements observed over years and lifetimes can reveal population and species-level patterns (Fig 6.1). These scales, from foraging trip through to species, are intrinsically linked and inter-connections can be drawn. For example, the foraging decisions of individuals can have ecological implications for populations, as it is at the individual level where natural selection operates.

Marine predators inhabit particularly patchy and hierarchical environments (Russell *et al.* 1992; Fritz *et al.* 2003) and scale is an important means to examine aspects of their ecology and how they forage (Hunt & Schneider 1987). Variability in movement patterns across a range of spatial and temporal scales is a further consideration as this directly affects the number of animals which need to be sampled, and over what time period, in order to address particular ecological questions (Hays *et al.* 2016). This study used movement data from a large number of animals (tracks of up to 184 Antarctic fur seals were included for some analyses) across multiple years and populations, which enabled the examination of habitat use and foraging ecology at a range of scales.

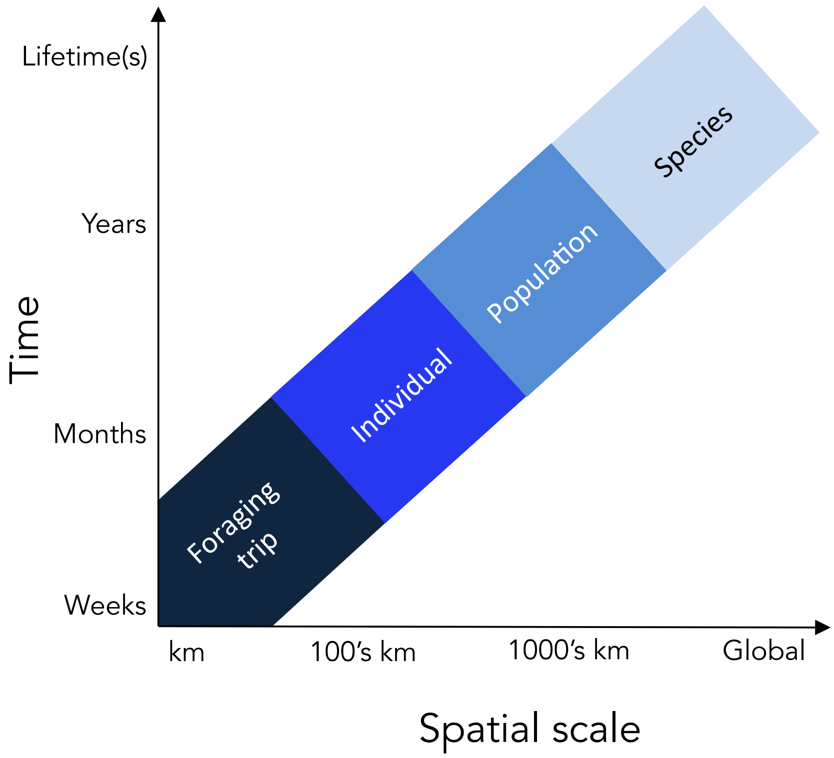

Figure 6.1. The relationship between the spatial and temporal scales of animal movement ecology. The y-axis represents movement observations spanning temporal scales from weeks to the lifetimes, while the x-axis represents spatial scales from kilometres to the globe.

Foraging strategies of individuals

A behavioural strategy is a somewhat abstract concept in ecology. It does, however, provide a framework to study how an animal's decisions affect its fitness and life history (Breed *et al.* 2011). Many behaviours and decisions are governed by strategies, but at the core of an animal's fitness is its foraging strategy (Stephens & Krebs 1986). Foraging strategies are often complex and the interpretation of them is dependent on the scales considered, which are often hierarchical in nature. Spatially, the capture of prey at fine scales is nested in a broader strategy of choice of foraging habitat or patch (Fauchald *et al.* 2000) and temporally, short-term strategies (e.g.

foraging trips) may be nested within an annual or lifetime strategy (McNamara & Houston 1986).

Foraging behaviour and resource use have traditionally been examined at the population or species level, with individuals considered as ecologically equivalent (Bolnick *et al.* 2003). However, individual variability in resource use (diet, foraging behaviour, habitat) is widespread in numerous vertebrate and invertebrate taxa from gastropods to mammals (for a review see Araújo *et al.* 2011). Such individual variability has implications for population dynamics and structure as well as species interactions (Hughes *et al.* 2008; Pruitt & Ferrari 2011). Furthermore, if individuals are not affected equally by perturbations in the environment there is a greater resilience of the population to disturbances (Lomnicki 1978). Niche variation within populations may buffer against habitat or resource loss and provide the genetic variation needed for adaptation to changing environments (Durell 2000), which has direct benefits for conservation biology through the preservation of intraspecific variation (Coates 2000).

SITE FIDELITY

In Chapter 2, the strategy of individual fidelity to oceanic foraging sites was assessed at broad spatial and temporal scales for Antarctic fur seals in the Southern Indian Ocean during their winter foraging migrations. While site fidelity was weak between successive trips within years, strong fidelity (on average >50% of the home range re-used, n=8) occurred between years. Individuals displayed distinct preferences for individually unique foraging habitat, which they returned to in the subsequent year. However, this strategy is not prevalent across all individuals in the population, with some animals being highly faithful to foraging habitats (n=5), while others did not re-use habitat (n=3). This appears to be a behaviour that is robust in some animals while not exhibited at all in others. Further research on a larger number of individuals across years will reveal the extent of this behavioural strategy.

Fidelity to foraging areas is common in a range of species from insects to mammals (Fresneau 1985; Schaefer *et al.* 2000), particularly when habitat quality or resource availability is stable or predictable (Andersson 1980). This is well documented in the marine environment: for example gannets, *Morus bassanus* (Hamer *et al.* 2001), Adelie penguins, *Pygoscelis adeliae* (Watanuki *et al.* 2003) and northern fur seals, *Callorhinus ursinus* (Call *et al.* 2008) during the breeding season. Conversely, Antarctic fur seals at Marion Island re-used areas that were highly variable, being characterized by a comparatively high long-term (multi-decadal) variance in sea surface temperature. Such sites are potentially allied with frontal regions and associated eddy fields and elevated long-term productivity (Moore & Abbott 2002). In a dynamic and patchy environment such as the Southern Ocean, consistent use of these areas will present an energetic advantage to individuals over the long-term (i.e. their lifetime) (Perry & Pianka 1997; Bradshaw *et al.* 2004a).

Strong between-year foraging site fidelity is rare for wide-ranging pelagic predators, as they typically have a diversity of habitats available for use. Long-term fidelity to foraging sites is a specialisation of some individuals within the Marion Island population and this inter-individual variability is likely to have population-level consequences through niche specialization and intra-specific competition (Bolnick *et al.* 2003). As the degree of individual foraging specialization in female Antarctic fur seals can vary among populations and within the annual cycle (Kernaléguen *et al.* 2015), whether Antarctic fur seals at other populations demonstrate the strategy of long-term foraging site fidelity identified here remains unclear. However, it is apparent that for a proportion of the Marion Island population winter foraging strategies and habitats are consistent over time. For tracking studies of marine predators, this is a rare insight as the majority of examinations are cross-sectional rather than longitudinal, providing little understanding of the longevity of particular behavioural strategies. This work highlights one of the benefits of large-scale, longer-term animal tracking programs.

DIVING BEHAVIOUR

The inter-individual variability in foraging strategy and habitat use was also reflected in the diving behaviour of Antarctic fur seals. Chapter 3 combined horizontal and vertical movement data to examine habitat use in three dimensions. A novel metric for otariid seals (broken-stick algorithm) quantified foraging effort within-dives at a much finer-scale than could be achieved from GLS horizontal tracking data alone. Diving behaviour was indicative of a seal's broader foraging trip strategy, with differences in dive behaviour (notably depth, duration, dive residual and diving effort) and foraging effort associated with two distinct foraging strategies within the Marion Island population. These strategies were to remain north of the Polar Front in waters relatively close to the colony, or transit south of the Polar Front to forage. Multiple strategies in movement patterns within populations of marine predators are not uncommon. For example, similar patterns of post-breeding habitat use have been observed in Harbor seals (*Phoca vitulina richardii*), with some animals migrating thousands of kilometres while other remained in waters local to breeding sites (Womble & Gende 2013). The costs and benefits of such alternate strategies are difficult to measure, but are usually assumed to be similar over the long-term; otherwise one would gain ascendancy over the other through natural selection

(Brockmann *et al.* 1979). In this study, however, the costs and benefits associated with the two strategies were able to be determined to some degree. Seals foraging south of the Polar Front had short and shallow dives with reduced dive and foraging effort, likely driven by improved access to vertically migrating prey as a result of the longer night durations in this region during winter and the relatively shallow distribution of the main prey in the region, Antarctic krill (*Euphausia superba*) (Nicol *et al.* 2000b; Walters 2014). The energetic costs accompanying this strategy include increased travel costs (Marginal Value Theorem, Charnov 1976) and the potential thermoregulatory requirements of using colder high Antarctic waters (Rutishauser *et al.* 2004). Seals remaining north of the Polar Front had deep, long dives and an elevated dive and foraging effort, yet minimal travel costs. The two divergent foraging strategies identified in Chapter 3 appear to currently co-exist in the Marion Island population, meaning neither strategy offers a significant long-term advantage in net energy gain. What remains unclear is if these two major strategies are consistent over time for individuals, as for the foraging site fidelity identified in Chapter 2, or whether animals demonstrate flexibility and utilise a combination of both.

Quantifying foraging behaviour is central to many animal movement and demographic studies. Given that the foraging behaviour of marine predators is difficult or impossible to observe directly, especially at sea, inferences have to be made. Area-restricted search (ARS) is a commonly inferred behaviour and is based on the premise that animals will increase their search effort in areas where resources are, or thought to be, plentiful (Kareiva & Odell 1987), as indicated by decreased travel speeds and increased path sinuosity in track data. In Chapter 3, ARS was measured in the more typical horizontal dimension using state-space models to infer unobservable behavioural states (see Jonsen *et al.* 2012), as well as the vertical dimension using a broken-stick algorithm (Heerah *et al.* 2014). This complimentary approach, which allows the testing of more sophisticated models of foraging behaviour than one dimension in isolation (Bestley *et al.* 2014), revealed a general agreement in ARS behaviour between the two dimensions. As vertical movement data is rarely available for a large number of animals (in this study the time-depth recorders used are significantly more expensive than the GLS tags), these results indicate that the use of horizontal movement data is appropriate to reveal the broader sub-surface behaviour patterns of Antarctic fur seals. Although the inclusion of vertical movements can provide greater insight into foraging activities, for studies without dive data the examination of track-based information alone can be appropriate to reveal foraging behaviours and habitats.

Habitat use of populations

Information on the habitat use of animals is critical for understanding ecosystems and for management and conservation. Chapter 4 examined the broad spatial distribution patterns of 184 Antarctic fur seals from three colonies. Species Distribution Models were developed in a generalized additive modelling framework using a comparative approach with environmental parameters relevant to the spatial scales that Antarctic fur seal populations are operating at. Considering the high levels of inter-individual variability in foraging ecology in the Marion Island population (Chapter 2 and 3) it was important to sample enough animals to account for this and provide an accurate representation of the spatial distribution of each colony. Previous studies have suggested a minimum sample size of approximately 20 individuals is adequate to assess spatial and temporal distributions for a population (Lindberg &

Walker 2007). For Antarctic fur seals, data from a minimum of ~50 foraging trips was needed to accurately reflect the at-sea movements of populations. This was realised at both Marion and Bird Island, but not at Cape Shirreff where fewer animals were sampled and seals ranged further.

FORAGING AREAS AND RELATIONSHIP WITH ENVIRONMENT

The models generally performed well in terms of deviance explained and cross-validation testing, and revealed the key environmental factors influencing Antarctic fur seal foraging habitat. This species inhabits an extremely dynamic environment (see Chapter 1) and colony locations span over 15 degrees of latitude from north of the Polar Front to south within the zone of winter sea ice. It is, therefore reasonable to expect that animals from different colonies are influenced by different oceanographic or environmental factors or respond differently to the same factors. Indeed the three populations in this study responded to different environmental parameters, reflecting regional oceanography and, presumably, prey availability.

The models were used to predict core habitats for each of the Marion Island, Bird Island and Cape Shirreff populations. Although these are the important habitats at a population level, examinations of the habitat use and foraging behaviour of individual seals assists in understanding these broad population movements. Chapter 2 showed that some seals use winter foraging areas repeatedly over the long-term. These areas are likely to be learnt by individuals and remembered, a useful tool for long-lived animals in temporally varied environments (Eliassen *et al.* 2007; Eliassen *et al.* 2009). Yet this individual-level memory is potentially nested within a broader population-level or colony preference (as represented by the spatial distribution of colonies), within which individual memory of patches is important (Bonadonna *et al.*

2001; Reid 2011). The investigation of fine-scale dive behaviour (Chapter 3) also aids in the interpretation of the broad-scale distribution of fur seal populations. For example, at Marion Island, important winter foraging habitat included local waters to the east of the colony as well as distant areas to the south, which have different associated costs and benefits in regards to prey availability and energy expenditure. As well as foraging areas that were unique to each population, Chapter 4 revealed areas of inter-colony overlap, indicating that some habitats can be important at the species level and could be considered more important from a management point of view (e.g. Montevecchi *et al.* 2012).

Environmental change and management

The movement patterns of marine predators can provide data necessary for the identification and mitigation of potential adverse human activities (Hays *et al.* 2016) and allow for the assessment of change in the distribution of populations and species (Louzao *et al.* 2013). In chapter 5, the historical spatial distribution of the Marion Island, Bird Island and Cape Shirreff Antarctic fur seal populations during winter over the last three decades was reconstructed using Species Distribution Models and long-term environmental data. This provided a baseline against which to assess changes to habitat over the past 20 years. At Cape Shirreff, the most southern breeding colony of Antarctic fur seals, a reduction in sea ice cover in recent decades is correlated with an increase in the availability of winter foraging habitat. Similar positive responses to reduced sea ice have been observed in other Antarctic predators at certain times of the year (Croxall *et al.* 2002; van den Hoff *et al.* 2014). However, as the standing stock of Antarctic krill, a fundamental trophic link in the Southern Ocean (Nicol 2006) and major dietary component of Antarctic fur seals in the Atlantic sector (Reid & Arnould

1996), is broadly linked to the extent of winter sea ice (Constable *et al.* 2003; Atkinson *et al.* 2004), the benefits of improved habitat accessibility may be moderated in the long term by potential changes to prey availability.

At both Marion and Bird Islands, habitat has remained relatively stable over recent decades, despite significant changes to the broader environment (water temperatures, winds and sea ice; Chapter 5) having potential impacts on the distribution of prey. It is possible that the flexible nature of Antarctic fur seals in response to environmental conditions (Lea *et al.* 2006) and prey (Green *et al.* 1991; Lea *et al.* 2002a; Walters 2014) allows animals to buffer against these changes during the unconstrained non-breeding period. Fur seals at Marion Island can be highly faithful to foraging areas (Chapter 2), so it is perhaps not surprising that the broad habitat use patterns of the colony overall have not shifted notably over this time. However, this fidelity raises questions about the ability of long-lived animals such as Antarctic fur seals (females can live up to 25 years in the wild, De Magalhaes & Costa 2009) to respond to future environmental change, particularly that which is rapid and occurs within the time frame of a single generation, or whether the inter-individual flexibility in foraging strategies demonstrated here (Chapters 2 and 3) will moderate any effects on populations overall.

The effective management of species often operates at the population level, relying on the monitoring and conservation of populations or meta-populations (see Noss 1990). Antarctic fur seal populations in the Southern Ocean are distinct from each other in many respects during winter, including in their habitat use and local environment (Chapter 4), the level of recent environmental and associated habitat change (Chapter 4), their foraging trip duration and number (Lea *et al.* unpublished data) and diet (Walters 2014). Consequently, the management and conservation of this species requires a population-based approach.

Aside from the spatial distribution data necessary for management, it is also important to understand temporal variation in habitats and behaviours (Game *et al.* 2009). In Chapter 5, seasonal habitat models documented considerable changes in the foraging habitats for all colonies across the non-breeding winter period. The low within-year site fidelity of individuals (Chapter 2) is reflected in these broader population movements and is related to a combination of animals responding to seasonal biophysical shifts in the environment over winter (e.g. sea ice extent) and evolving energetic requirements associated with breeding phase (e.g. Weimerskirch *et al.* 1993).

Spatio-temporal information permitted an assessment of the winter habitat use of Antarctic fur seals, an indicator species in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP, CCAMLR 2013a), in relation to management areas and overlap with fisheries activities. The core foraging habitats of all three populations coincided with high fishing effort in certain management areas at different periods of the year, suggesting the potential exists for competition for prey resources between this species and Southern Ocean fisheries during the non-breeding season. Given recent proposals for a system of marine protected areas (MPAs) in the Southern Ocean (Delegations of Australia and France 2011; Delegations of Australia, France and the European Union 2013; Delegations of New Zealand and the USA 2013), this information could be used in the design and evaluation of MPAs (see Halpern 2014). These may be static in nature (e.g. movements of Adelie penguins were used to justify, in part, the establishment of a high-seas MPA, CCAMLR 2009), or dynamic closures better suited to protecting shifting habitats (see Hobday *et al.* 2013; Lewison *et al.* 2015) like those shown here for Antarctic fur seals. Furthermore, the substantial use of habitat outside of the CCAMLR Convention Area indicates there are likely to be factors influencing Antarctic fur seals that are occurring outside of the management area, but within other management zones. This provides an important context for the assessment of fisheries and climate impacts on wide-ranging species such as Antarctic fur seals during winter and interpretation of monitoring parameters within the CCAMLR framework.

Perspectives

Through a suite of bio-logging and modelling approaches, this study has produced substantial new insights into the ecology of a key Southern Ocean predator during the non-breeding winter period. The examination of habitat use and foraging behaviour at a range of ecological scales has revealed new information at the individual, population and species levels. By considering these inter-relationships, we are now able to better understand how Antarctic fur seals utilise their Southern Ocean habitats during winter and how foraging strategies such as site fidelity and diving behaviour affect habitat use and management of the species. The extensive range of foraging habitats and their importance at certain periods of the winter, particularly pre- and post-breeding, reveals some management challenges. The findings of this study are relevant not only to Antarctic fur seals, but have broader applications for understanding the foraging behaviours of marine predators and management implications for Southern Ocean and other marine ecosystems.

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